THE SYSTEMATICS AND ZOOGEOGRAPHY OF THE UNIONIDAE (MOLLUSCA: BIVALVIA) OF THE SOUTHERN ATLANTIC SLOPE REGION

RICHARD I. JOHNSON

CONTENTS

ABSTRACT

The Atlantic Slope region consists of those streams flowing into the Atlantic Ocean from the Altamaha River system, Georgia, to the lower St. Lawrence River system, Canada, including rivers in Newfoundland and Labrador. Forty species comprise the unionid fauna. Most of the species that are clearly of Interior Basin origin are a northern group that migrated around the northern end of the Appalachian Mountains before the Pleistocene; there is a southern group that entered the Atlantic Slope region through a confluence of the Apalachicola and Savannah river systems, also in pre-Pleistocene time; there is also an additional fauna originally of Interior Basin origin, but whose ancestry is more remote.

INTRODUCTION

The Unionacea and Mutelacea (Parodiz and Bonetto, 1963), or freshwater mussels, are found throughout the world, but it is in the Mississippi River system that the Unionidae have especially radiated and achieved their greatest diversity. This, the *Interior Basin*, embraces 1,200,000 square miles. The rivers are very old, and flow over vast limestone beds. Here is found a variety of shell forms which is rivaled only in a few species found in the rivers of

China. Within the Interior Basin, H. and A. van der Schalie (1950: 450) recognized the *Ozark* and *Cumberland* regions, each of which has an indigenous unionid fauna of its own, as well as the Interior Basin one.

Continental North America is made up of the following additional regions. They are given essentially as defined by H. and A. van der Schalie (1950). The *Pacific* region is the area west of the Rocky Mountains. It has a very limited unionid fauna, which is clearly of Asiatic origin. Found there are several species of *Anodonta*, *Margaritifera margaritifera* (Linnaeus), and *"Gonidea" angulata* (Lea), which may belong to the Asiatic genus *Solenaia* Conrad.

The *West Gulf Coastal* region consists of the streams flowing into the Gulf of Mexico from the eastern slope of Mexico north to, but not including, the Alabama-Coosa River system. Found there are several endemic genera of Unionidae. It has been tentatively suggested by both Simpson (1892: 406) and H. and A. van der Schalie (1950: 452) that this might be regarded as a subregion of the Interior Basin.

The *Apalachicolan* (or *West Floridian*) region was mentioned by H. and A. van der Schalie (1950: 450) and is now defined as consisting of those river systems flowing into the Gulf of Mexico from the Escambia to the Suwannee, and also including the St. Marys and the Satilla, which flow directly into the Atlantic Ocean.

Peninsular Florida has representatives of only six genera. These consist of species derived mostly from the Apalachicolan and Atlantic Slope regions. This area will be discussed as a separate region in a subsequent report.

The *Atlantic Slope* region includes the river systems flowing into the Atlantic Ocean from the Altamaha, Georgia, to the lower St. Lawrence, Canada, as well as those of Newfoundland and Labrador. The Unionidae of this region are of Interior Basin origin, but on the Atlantic slope the species are smaller and are neutral in color. Yet, the only two species of Unionidae with true spines, *Elliptio spinosa* (Lea) and *Pleurobema collina* (Conrad), occur here.

Because the Atlantic Slope region has distinct northern and southern assemblages of species, it has been divided here into the *Southern Atlantic Slope* region, which extends from the Altamaha River system, Georgia, to the James River system, Virginia, and the *Northern Atlantic Slope* region, which extends from the York River system, Virginia, to the lower St. Lawrence River system, Canada. Between the York River and the glacial drift border (roughly along the Pennsylvania-New York boundary) are found all of the Unionacea that repopulated the Northern Atlantic Slope region north of the limit of glacial drift.

The Unionacea, or freshwater mussels, offer two advantages for zoogeographic study: 1) As shown in the systematic portion of this paper, there are a reasonable number of species, most of which are clearly distinguishable, and whose generic affinities have been revealed rather clearly by Ortmann (1911; 1912a). 2) They have a limited mode of distribution, being unable to pass over land from one drainage system to another. Their ability to move between drainage systems is dependant on the mobility of fishes to which the glochidia attach themselves. Of the primary freshwater fishes, Myers (1938: 343) stated,

> "They are inescapably confined to their own particular drainage systems and can migrate from one isolated stream basin to the next only through the slow physiographical change of the land itself (stream capture, etc. [baseleveling])."

For this reason the distribution of the Unionacea gives evidence of former stream confluences and of flooding in baseleveled coastal regions.

Van der Schalie (1945) convincingly illustrated the use of Unionidae as a means of tracing major stream confluences. He also reviewed the old controversy over mechanical distribution, which implies that

unionid distribution is haphazard and fortuitous, caused by aquatic birds to whose feet gravid females may occasionally become attached. This theory postulates that the shell will be carried to a different river system, and that there the glochidia will be released and will find a *suitable* host fish. No one has actually established that Unionidae have been successfully spread by birds in this manner, but even granting this possibility, there is no evidence that it is, or was, an important method of distribution, since zoogeographic data fail to substantiate unionid distribution by any agent other than fish.

In their discussion of the freshwater mollusks of the Apalachicolan region, Clench and Turner (1956: 103) support the idea that that fauna was distributed by mechanical means, though they are vague as to what those means might have been. Exception is taken here to their theory of distribution, but *only* as far as the Unionacea are concerned.

The Apalachicolan Unionacea were restudied, and it is demonstrated here that their general distribution is not fortuitous. References are made to some of the Unionidae of the Alabama-Coosa River system to illustrate the origin of some of the Apalachicolan species and to illuminate the sequence of stream captures which affected the distribution of both Apalachicolan and Southern Atlantic Slope Unionidae.

In his classic study of the influence of the Alleghenian Divide on the distribution of mollusks and crayfish, Ortmann (1913a) assumed that the Unionidae were distributed by natural means. Both by choice and because of the confusion in which he found the systematics of the southern species, his work was limited to the Atlantic side of the divide, primarily to the species of Unionacea found on the Northern Atlantic slope.

In the present study, the distribution of the Apalachicolan and Atlantic Slope Unionacea is analyzed, and, with the exception of *Margaritifera margaritifera* (Linnaeus), *Alasmidonta marginata* (Say), and *Anodonta cataracta fragilis* (Lamarck), which are beyond the scope of this paper, all of the Atlantic Slope Unionacea are included and their nomenclature is revised.

ACKNOWLEDGMENTS

In 1961, Dr. William J. Clench, my longtime mentor, received a grant from the National Science Foundation (G18922) to make a collection of the freshwater mollusks of the Atlantic Slope of Georgia. Upon completion of the expedition, he generously gave me the Unionidae for study. As the study progressed, it gradually became apparent that the unionids of the entire Southern Atlantic slope had to be included if the work was to be of any significance.

The opportunity for examining relevant types was provided by: Dr. Norman Tebble, British Museum (Natural History); Dr. Gilbert Ranson, Paris Museum; Dr. G. Mermod, Geneva Museum; Dr. Arthur H. Clarke, Jr., National Museum of Canada; Dr. David H. Stansbery, Ohio State Museum; Dr. Juan Parodiz, Carnegie Museum, Pittsburgh; Dr. R. Tucker Abbott, Academy of Natural Sciences of Philadelphia; Dr. Henry van der Schalie, Museum of Zoology, University of Michigan. Drs. Harold Rehder, Joseph Rosewater, and Joseph Morrison, United States National Museum, kindly permitted me to study the collections under their care and to borrow *all* relevant types. The cost of photographing the types was generously borne by the William F. Milton Fund, Harvard University.

Dr. Ruth Patrick, Academy of Natural Sciences of Philadelphia, made available the Unionidae collected for her by John N. Bates and Samuel L. H. Fuller; Mr. Bates allowed me to study the portion of this material under his care at the Museum of Zoology, University of Michigan. Dr. Patrick kindly deposited most of the

material collected by Mr. Fuller in the Museum of Comparative Zoology.

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PART I. THE ZOOGEOGRAPHY OF THE UNIONACEA OF THE APALACHICOLAN AND ATLANTIC SLOPE REGIONS

CHAPTER 1

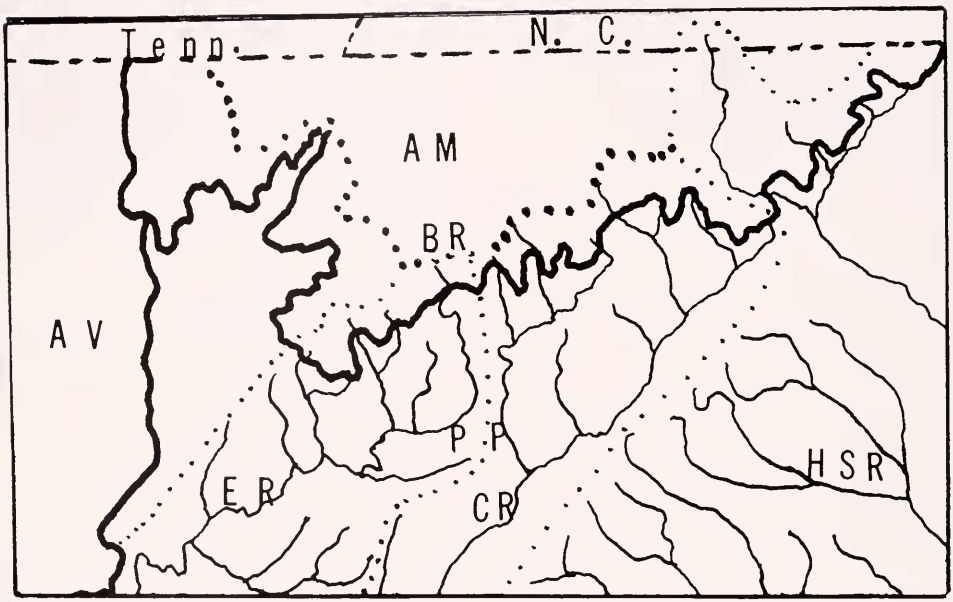
The distribution of the Unionacea in the Apalachicolan region as evidence of a former confluence of the headwaters of the Alabama-Coosa, Apalachicola, and Savannah river systems.

Figure 1 illustrates the propinquity of the headwaters of the Alabama-Coosa, Apalachicola, and Savannah river systems. Van der Schalie (1945) made it clear that there was once a connection between the Tennessee and Alabama river systems; this connection is of interest here since certain unionid species of the Alabama-Coosa River system are discussed in this paper. Matteson (1948a: 131) following, in part, Hayes and Campbell (1894), suggested that in the late Tertiary, the Chattahoochee River of the Apalachicola River system captured a tributary of the Etowah River, of the Alabama-Coosa River system, and that the Savannah River then captured one of the tributaries of the Chattahoochee River. This present study supports these geomorphological assertions, but in a different order. The distribution of Apalachicolan species in the Savannah River system seems to indicate that this system may first have been connected to, and later separated from, the Chattahoochee River before the latter was connected to the Alabama-Coosa River. These conditions would explain why certain species found in both the Alabama-Coosa and Apalachicola river systems are absent in the Savannah River system.

To understand the origins of the Unionidae of the Southern Atlantic Slope, it was necessary to study the distribution of the superfamily Unionacea in the Alabama-Coosa and Apalachicola river systems. Further, the whole Apalachicolan region had to be considered, to determine if it could be established that unionid distribution there is not fortuitous.

The Apalachicolan region defined. This region is regarded here as consisting of the river systems flowing into the Gulf of Mexico, from the Escambia to the Suwannee. Also included are the St. Marys and Satilla, although they flow into the Atlantic Ocean (Plate 1), because, as Table 1 shows, their modest unionid faunas consist entirely of species found in the Apalachicolan region, and further, because *Elliptio crassidens crassidens* and *E. c. downiei* occur in them, respectively, and are dominant.

According to Cooke (1945: 273), in the early Pleistocene, during the Aftonian interglacial stage when the Brandywine terrace (Citronelle Formation in the Southeast) was formed, the sea level was 270 feet above the present level. If this were so, most of the area occupied by the present St. Marys and Satilla river systems, and virtually all of Peninsular Florida, were inundated, with the exception of



Text-figure 1. Northern Georgia, illustrating the propinquity of the headwaters of the Etawah River (ER), of the Alabama-Coosa; of the Chattahoochee River (CR), of the Apalachicola; and of the Savannah (HSR) river systems. The topographic areas are the Appalachian Mountains (AM), Appalachian Valley (AV), and the Piedmont Plateau (PP). The Blue Ridge divide (BR) is indicated by large dots. The minor divides are indicated by smaller dots. (After Keith, 1925, pl. 29.)

several small islands in the vicinity of present Polk County (Cooke, 1945: 273).[1]

It is now generally agreed that this flooding took place in the Upper Miocene (Alt and Brooks, 1965: 408).

MacNeil (1950: 98, 99) casts doubt on Cooke's evidence on the extent of Aftonian flooding, and on the basis of his identification of marine terraces concludes that the Citronelle Formation is of subaerial origin, and that there is no evidence to indicate that the sea ever transgressed it to an altitude of more than 150 feet during the Yarmouth interglacial stage. This flooding is now thought to have occurred during the Pliocene. MacNeil's detailed map (pl. 19) shows that even at 150 feet Peninsular Florida was reduced to a number of small islands where a unionid fauna might have had refugia. In any case, except for a small portion of the Satilla River which is above the area of maximum flooding, the remainder of it, and all of the St. Marys River, is of more recent origin (see p. 289).

It is assumed that these two rivers were mostly repopulated from the west. The appearance of *Elliptio c. crassidens* in the Pliocene of Florida (see note on p. 271) indicates that it has been present in this general area over a long period of time.

Analysis of the distribution of the species.

The Apalachicolan and Atlantic Slope regions consist of a number of independent river systems, some with quite different faunas. Table 1 shows all of the Unionacea known from the individual Apalachicolan river systems, systematically arranged. Some differences in species concepts and

[1] Orange (Ocala) Island, referred to by Clench and Turner (1956: 104), was a land mass that was separated from the continent by the Suwannee Strait during the late Oligocene (Vaughan, 1910: 156), and its existence appears to have had no bearing on the present unionid fauna.

TABLE 1. DISTRIBUTION OF THE UNIONACEA OF THE APALACHICOLAN REGION AND RELEVANT SPECIES OF THE ALABAMA-COOSA RIVER SYSTEM.

Alabama-Coosa River system		Escambia River system	Yellow River system	Choctawhatchee River system	Apalachicola River system	Ochlockonee River system	Suwannee River system	St. Marys River system	Satilla River system
	1. *Margaritifera hembeli* (Conrad)	×							
1/	2. *Fusconaia succissa* (Lea)	×	×	×					
	3. *Fusconaia escambia* Clench & Turner	×	×						
	4. *Quincuncina infurcata* (Conrad)				×	×	×		
	5. *Quincuncina burkei* Walker			×					
×	6. *Amblema boykiniana* (Lea)	×			×	×			
	7. *Amblema neisleri* (Lea)				×				
×	8. *Amblema perplicata** (Conrad)	×	×						
2/	9. *Pleurobema strodeanum* (Wright)	×	×	×					
	10. *Pleurobema pyriforme* (Lea)				×	×	×		
×	11. *Elliptio crassidens crassidens* (Lamarck)	×			×			×	
	12. *Elliptio crassidens downiei* (Lea)								×
	13. *Elliptio fraterna* (Lea)			×	×				
3/	14. *Elliptio complanata* (Lightfoot)				×				
	15. *Elliptio icterina* (Conrad)	×	×	×	×	×	×	×	
×	16. *Elliptio arctata* (Conrad)	×	×		×				
	17. *Elliptio lanceolata* (Lea)	×			×				×
	18. *Elliptio jayensis* (Lea)					×	×		
	19. *Elliptio nigella* (Lea)*				×				
	20. *Elliptio chipolaensis* (Walker)				×				
	21. *Elliptio sloatiana* (Lea)				×	×			
×	22. *Uniomerus tetralasmus* (Say)	×	×	×	×	×	×		
4/	23. *Alasmidonta triangulata* (Lea)				×				
	24. *Alasmidonta wrightiana* (Walker)*					×			
×	25. *Anodonta grandis* Say			×	×	×			
×	26. *Anodonta cataracta cataracta* Say			×	×				
×	27. *Anodonta imbecilis* Say	×			×	×			
	28. *Anodonta peggyae* Johnson*			×	×	×	×		
	29. *Anodonta couperiana* Lea				×	×		×	
	30. *Anodonta suborbiculata* Say*	×							
×	31. *Anodontoides radiatus* (Conrad)*	×			×				
×	32. *Strophitus subvexus* (Conrad)*				×				
5/	33. *Obovaria rotulata* (Wright)*	×							
×	34. *Carunculina parva* (Barnes)	×	×	×	×	×	×		
×	35. *Villosa vibex* (Conrad)	×	×	×	×	×	×		
×	36. *Villosa lienosa* (Conrad)	×	×	×	×	×	×		
	37. *Villosa choctawensis* Athearn*			×					
	38. *Villosa villosa* (Wright)				×	×	×	×	
×	39. *Lampsilis excavatus* (Lea)	×							
×	40. *Lampsilis claibornensis* (Lea)	×	×	×	×	×	×		
	41. *Lampsilis haddletoni* Athearn*			×					
	42. *Lampsilis binominatus* Simpson*				×				
×	43. *Lampsilis anodontoides* (Lea) (6)	×		×	×	×	×		
	44. *Lampsilis australis* Simpson	×		×					
	45. *Lampsilis jonesi* van der Schalie*			×					

TABLE 1. (*Continued*)

Alabama-Coosa River system		Escambia River system	Yellow River system	Choctawhatchee River system	Apalachicola River system	Ochlockonee River system	Suwannee River system	St. Marys River system	Satilla River system
	46. *Lampsilis subangulata* (Lea)				×	×			
×	47. *Medionidus penicillatus* (Lea)				×				
	48. *Medionidus walkeri* (Wright) (7)				×	×	×		
×	49. *Glebula rotundata* (Lamarck)	×			×				
	TOTAL NUMBER OF SPECIES	23	11	18	33	20	13	4	2

* (See Johnson, 1965; 1967b,c; 1968; 1969a). *A. perplicata* (Conrad) has not been previously published on as part of the Apalachicolan fauna. It has been found in the Escambia River, Pine Barren, Escambia Co., Florida, and in Picket Retch Lake [not located, but presumed to be in the Yellow River system], Walton Co., Florida.

1. *Fusconaia*, represented by several species.
2. *Pleurobema rubellum* (Lea).
3. *Elliptio dilatata* (Rafinesque) see p. 279.
4. *Alasmidonta mccordi* Athearn (1964: 134, pl. 9, figs. a–b). Not close to *Alasmidonta s.s.*
5. *Obovaria unicolor* (Lea).
6. Clench and Turner (1956: 158), following Simpson (1914: 91), recognize *floridensis* (Lea) as a subspecies of *Lampsilis anodontoides* (Lea) = *teres* (Rafinesque), but admit that "young specimens of the typical form would be difficult to separate from this subspecies." It is true that specimens of this species tend to be smaller and thinner toward the southern end of its range, but *floridensis* is not a subspecies as this concept is currently understood. It was described as: *Unio floridensis* Lea 1852. Trans. Amer. Philos. Soc. 10: 274, pl. 21, fig. 31 [Cháctáhachi River, West Florida, figured holotype ANSP 42081. Clench and Turner (1956: 202) restricted the type locality to the Choctawhatchee River, 1 mi. W Caryville, Holmes Co., Florida]. Lea, 1852, Obs. Unio, 5: 30.
7. Clench and Turner (1956: 189, pl. 6, fig. 7), under the name *Medionidus penicillatus* (Lea), described and figured *Medionidus walkeri* (Wright), a species endemic to the Apalachicolan region having a well defined posterior ridge and a posterior slope with strong corrugations that run from the posterior ridge to the posterior margin.

Medionidus penicillatus (Lea), though found in the Apalachicolan region, is more common in the Alabama-Coosa River system. It has a very rounded posterior ridge, and a posterior slope that has, when sculpture is present, small, slightly curved folds that run from the posterior ridge to the posterior margin. It was described as: *Unio penicillatus* Lea 1857, Proc. Acad. Nat Sci. Phila., 9: 171 (Chattahoochee River, near Columbus [Muscogee Co.]; [Chattahoochee River], near Atlanta [De Kalb Co.]; Flint River near Albany, [Dougherty Co.]; *all* Georgia). Lea, 1859, Jour. Acad. Nat. Sci. Phila., ser. 2, 4: 203, pl. 23, fig. 85, figured holotype USNM 84142 from the Flint River. Clench and Turner (1956: 190) restricted the type-locality to the Chattahoochee River, near Columbus). Lea, 1859, Obs. Unio., 7: 21.

nomenclature from that of Clench and Turner (1956) were noted by Johnson (1965; 1967b, 1967c; 1968; 1969a); the remainder are discussed in the notes to Table 1, or in the systematic portion of this paper.

Because of its former connection with the Tennessee River, the unionid fauna of the Alabama-Coosa River system is extensive. Only those genera and species that seem germane to the understanding of the distribution of the Unionacea of the Apalachicolan and Atlantic Slope regions are included here.

Forty-nine species comprise the unionid fauna of the Apalachicolan region (Table 1); nineteen species have affinities with species to the west, twelve are endemic to the region, and eleven more are restricted to individual river systems. Three species, which were probably originally endemic to the Apalachicolan region, have spread into the Atlantic Slope region, and four others have spread in the opposite direction.

Six Apalachicolan unionids are so ubiquitous throughout the region (Table 1, A) that they offer no clues as to their method of distribution. *Amblema perplicata* (Conrad) is found in rivers flowing into the Gulf of Mexico from central Texas to the Yellow River system, Florida, and in the west, north to river systems in Arkansas and Missouri. It is close to *A. plicata* (Say), which is widely distributed throughout the Interior Basin. *Lampsilis excavatus* ranges uniformly from the Pearl River, Mississippi, to the Escambia River system, Florida. *Margaritifera hembeli*, a member of the family Margaritiferidae, appears to be a relict. It is found in one other drainage, the Bayou Teche, Louisiana, in the West Gulf Coastal region. *Anodonta suborbiculata* is widely distributed throughout the Interior Basin.

TABLE 1, A. UNIONACEA, DERIVED FROM THE WEST, FOUND IN THE ALABAMA-COOSA RIVER SYSTEM, AND WHICH TERMINATE IN THE APALACHICOLAN REGION, OR ARE WIDELY DISTRIBUTED THROUGHOUT AND BEYOND IT.

	Escambia River system	Yellow River system	Choctawhatchee River system	Apalachicola River system	Ochlockonee River system	Suwannee River system	St. Marys River system	Satilla River system	Peninsular Florida	Southern Atlantic Slope
U. tetralasmus	×	×	×	×	×	×			×	×
C. parva	×	×	×	×	×	×			×	
L. claibornensis	×	×	×	×	×	×				
V. vibex	×	×	×	×	×	×			×	
V. lienosa	×	×	×	×	×	×			×	×
L. anodontoides	×	×	×	×	×	×			×	
A. perplicata	×	×								
L. excavatus	×									
M. hembeli	×									
A. suborbiculata	×									

Nine species of the Alabama-Coosa River system (Table 1, B) appear to have reached the Apalachicola River through a former stream confluence (Text-fig. 1, see p. 285), since they are mostly missing from intervening systems. With the probable exception of *Anodonta grandis*, *A. imbecilis*, and *Glebula rotundata*, it is possible that the remaining six species were once endemic to the Alabama-Coosa River system. Matteson (1948a: 131) suggests that *Elliptio c. crassidens* and *E. dilatata* Rafinesque (figured by Ortmann, 1919: 95, pl. 8, fig. 2) reached the Interior Basin from the Alabama-Coosa River system. If this can be shown, then *Elliptio s. s.* is a genus originally from the coastal regions.

Four species of Unionidae appear to have reached the Apalachicolan region from a former confluence of the Apalachicola and Savannah river systems (Table 1, C). They will be discussed with the Southern Atlantic Slope fauna. Three additional species entered the Savannah

TABLE 1, B. UNIONIDAE, DERIVED FROM THE WEST, FOUND IN BOTH THE ALABAMA-COOSA AND APALACHICOLA RIVER SYSTEMS, SUPPORTING THE ASSUMPTION OF A FORMER CONFLUENCE BETWEEN THEM.

	Alabama-Coosa River system	Escambia River system	Yellow River system	Choctawhatchee River system	Apalachicola River system	Ochlockonee River system	Suwannee River system	St. Marys River system	Satilla River system	Peninsular Florida
E. crassidens	×	×			×			×		×[1]
A. boykiniana	×	×			×	×				
A. grandis	×			×	×	×				
A. imbecilis	×	×			×	×				
E. arctata	×	×	×		×					
A. radiatus	×	×			×					
S. subvexus	×				×					
G. rotundata	×	×			×					
M. penicillatus	×				×					

[1] *E. crassidens* has been found as a fossil in the Pliocene deposits of St. Petersburg, Hillsboro Co., Florida. It was renamed *Elliptio pachyodon* Pilsbry (see p. 306).

TABLE 1, C. UNIONIDAE, DERIVED FROM THE EAST OR WEST, FOUND IN THE ALABAMA-COOSA AND APALACHICOLA RIVER SYSTEMS, AND WHICH GIVE EVIDENCE OF A FORMER CONFLUENCE WITH THE SAVANNAH RIVER SYSTEM, INCLUDING THE POSTULATION OF TWO MINOR STREAM CONFLUENCES.

		Alabama-Coosa River system	Escambia River system	Yellow River system	Choctawhatchee River system	Apalachicola River system	Ochlockonee River system	Suwannee River system	St. Marys River system	Satilla River system	Peninsular Florida	Savannah River system
From West	*E. icterina*		×	×	×	×	×	×	×		×	×
From East	*E. complanata*					×						×
From East	*A. c. cataracta*	×			×	×						×
From East	*A. couperiana*					×	×		×		×	×
From East	*E. lanceolata*		×			×				×		×
From West	*E. fraterna*				×	×						×
From West	*A. triangulata*					×						×

River from the Apalachicola River system: *Elliptio icterina*, which is abundant throughout the Apalachicolan region; *Elliptio fraterna*, which is dominant in the Choctawhatchee River system; and *Alasmidonta triangulata*, which seems to be more abundant in the Apalachicola than in the Savannah River. It probably cannot be determined whether the six species discussed moved from east to west, or from west to east, but their distribution by stream confluence is evident.

Two additional cases of stream capture are postulated: 1) The abundance of *Anodonta cataracta* in Uphauppee Creek of the Alabama-Coosa River system and its presence in Uchee Creek of the Apalachicola River system suggest the possibility of a former connection here, where *Anodonta cataracta*, *A. imbecilis*, *Elliptio arctata*, *Strophitus subvexus*, and *Anodontoides radiata* could also have passed from one river system to the other (Plate 1, C). 2) The presence of *Anodonta cataracta* in the Choctawhatchee River system and *Elliptio fraterna* in the Chattahoochee River system argues for a former commingling of the headwaters of the Choctaw-

TABLE 1, D. UNIONIDAE MOSTLY ENDEMIC TO THE APALACHICOLAN REGION AND PENINSULAR FLORIDA.

	Escambia River system	Yellow River system	Choctawhatchee River system	Apalachicola River system	Ochlockonee River system	Suwannee River system	St. Marys River system	Satilla River system	Peninsular Florida
V. villosa				×	×	×	×		×
A. peggyae			×	×	×	×			×
E. jayensis						×			×
M. walkeri				×	×	×			
P. pyriforme				×	×	×			
Q. infurcata				×	×	×			
L. subangulata				×	×				
E. sloatiana				×	×				
F. succissa	×	×	×						
P. strodeanum	×	×	×						
L. australis	×	×							
F. escambia	×	×							

Table 1, E. Unionidae endemic to individual river systems in the Apalachicolan region.

	Escambia River system	Yellow River system	Choctawhatchee River system	Apalachicola River system	Ochlockonee River system	Suwannee River system	St. Marys River system	Satilla River system
E. crassidens downiei								×
A. wrightiana					×			
L. binominatus				×				
E. nigella				×				
E. chipolaensis				×				
A. neisleri				×				
Q. burkei			×					
L. haddletoni			×					
L. jonesi			×					
V. choctawensis			×					
O. rotulata	×							

hatchee River with a tributary of the Chattahoochee River (Plate 1, D).

The unionid species that are endemic to the Apalachicolan region and Peninsular Florida show an orderly pattern of distribution (Table 1, D). While major stream confluences can be demonstrated, and minor ones only inferred, the analyses of Tables 1, A-D, argue convincingly, though heuristically, that the distribution of the Unionidae is not fortuitous, and that no method of dispersal other than the natural one need be postulated.

The great number of endemic species in individual river systems (Table 1, E) is evidence that this portion, at least, of the fauna is old, an observation made by Clench and Turner (1956: 104). The floodings of the coastal plain and lower upland country during the Pliocene and Pleistocene limited endemism to the larger river systems. Thus the lack of any endemic species in the Yellow River system (Table 1) is explained by inundation. It was subsequently repopulated by species from the Escambia and Choctawhatchee River systems.

CHAPTER 2

The distribution of the Unionidae in the Southern Atlantic Slope region as evidence of a former stream confluence of the headwaters of the Apalachicola and Savannah river systems.

The Atlantic Slope region defined and subdivided. This region consists of those streams flowing into the Atlantic Ocean from the Altamaha River system, Georgia, to the lower St. Lawrence River system, Canada, and also including Newfoundland and Labrador, since, at least, *M. margaritifera* and *A. cataracta fragilis* persist north of the St. Lawrence. The area can be subdivided into a Southern and Northern region, since the unionid fauna consists of an assemblage of species of both southern and northern origin.

The Southern Atlantic Slope region extends from the Altamaha River system, Georgia, to the James River system, Virginia, for this is the last river system to the north with a clearly southern assemblage of species. *The Northern Atlantic Slope region*, as regarded here, begins with the York River system, since, with the probable exception of *E. lanceolata*, the remaining six species are all part of the northern fauna (see Table 2). As discussed previously, the St. Marys and Satilla river systems to the south of the Altamaha River system are regarded as part of the Apalachicolan region.

TABLE 2. DISTRIBUTION OF THE UNIONIDAE OF THE ATLANTIC SLOPE REGION FROM THE ALTAMAHA TO THE POTOMAC RIVER SYSTEMS, AND RELEVANT SPECIES FOUND IN THE APALACHICOLA RIVER SYSTEM.

Apalachicola River system		Altamaha River system	Ogeechee River system	Savannah River system	Edisto River system	Cooper-Santee River system	Pedee River system	Waccamaw River system	Cape Fear River system	Neuse River system	Pamlico River system	Roanoke River system	Chowan River system	James River system	York River system	Rappahannock River system	Potomac River system
	1. *Pleurobema collina* (Conrad)										×			×			
	2. *Pleurobema masoni* (Conrad)		×	×			×		×	×	×	×	×	×			
	3. *Elliptio spinosa* (Lea)	×															
	4. *Elliptio congaraea* (Lea)		×	×	×	×	×		×								
	5. *Elliptio waccamawensis* (Lea)							×									
	6. *Elliptio dariensis* (Lea)	×															
×	7. *Elliptio fraterna* (Lea)			×													
×	8. *Elliptio complanata* (Lightfoot)	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×
	9. *Elliptio hopetonensis* (Lea)	×															
×	10. *Elliptio icterina* (Conrad)	×	×	×	×	×	×	×	×								
×	11. *Elliptio arctata* (Conrad)			×		×			×								
×	12. *Elliptio lanceolata* (Lea)	×	×	×	×	×	×		×	×	×	×	×	×	×	×	×
	13. *Elliptio shepardiana* (Lea)	×															
×	14. *Uniomerus tetralasmus* (Say)	×	×	×	×	×	×	×	×	×	×	×	×				
	15. *Lasmigona subviridis* (Conrad)			×		×	×		×	×	×			×	×	×	×
	16. *Alasmidonta heterodon* (Lea)									×						×	×
	17. *Alasmidonta undulata* (Say)					×	×		×	×	×		×	×	×	×	×
×	18. *Alasmidonta triangulata* (Lea)		×	×		×											
	19. *Alasmidonta arcula* (Lea)	×															
	20. *Alasmidonta varicosa* (Lamarck)			×		×			×					×			×
×	21. *Anodonta cataracta cataracta* Say	×		×		×	×	×	×	×		×	×	×			×
	22. *Anodonta implicata* Say																×
	23. *Anodonta gibbosa* Say	×															
×	24. *Anodonta imbecilis* Say	×	×	×		×	×		×				×				
×	25. *Anodonta couperiana* Lea	×		×	×	×			×								
	26. *Strophitus undulatus* (Say)			×		×			×	×	×	×	×	×	×	×	×
	27. *Carunculina pulla* (Conrad)	×		×		×			×	×							
×	28. *Villosa vibex* (Conrad)	×	×	×	×	×	×	×	×	×							
	29. *Villosa delumbis* (Conrad)	×	×	×	×	×	×	×	×	×							
	30. *Villosa constricta* (Conrad)					×			×	×	×	×		×			
	31. *Ligumia nasuta* (Say)													×			×
	32. *Lampsilis cariosa* (Say)		×	×		×		×	×	×	×		×		×	×	×
	33. *Lampsilis dolabraeformis* (Lea)	×															
	34. *Lampsilis ovata* (Say)																×
	35. *Lampsilis ochracea* (Say)			×				×			×			×	×	×	×
	36. *Lampsilis radiata radiata* (Gmelin)						×				×	×					×
	37. *Lampsilis splendida* (Lea)	×	×	×		×											
11	TOTAL NUMBER OF SPECIES	18	12	21	8	20	13	9	19	14	12	8	9	12	7	8	14

TABLE 2, A. UNIONIDAE, MOST OF WHICH ARE WIDELY DISTRIBUTED IN THE NORTHERN ATLANTIC SLOPE REGION, ALL BUT ONE OF WHICH TERMINATE IN THE SOUTHERN ATLANTIC SLOPE REGION, BUT ARE OF DIVERSE ORIGINS.

	Altamaha River system	Ogeechee River system	Savannah River system	Edisto River system	Cooper-Santee River system	Pedee River system	Waccamaw River system	Cape Fear River system	Neuse River system	Pamlico River system	Roanoke River system	Chowan River system	James River system	York River system	Rappahannock River system	Potomac River system
A. implicata																×
L. nasuta													×			×
A. heterodon									×						×	×
L. radiata radiata						×		×		×						×
A. undulata					×	×		×	×	×		×	×	×	×	×
S. undulatus			×		×			×	×	×	×	×	×	×	×	×
L. subviridis			×		×	×		×	×	×			×	×	×	×
A. varicosa			×		×			×					×			×
L. cariosa			×				×			×	×		×	×		×
L. ochracea		×	×		×		×	×	×	×		×		×		×

Analysis of the distribution of the species (Table 2). All of the species of Unionacea found in the Atlantic Slope region are covered in this paper except *Margaritifera margaritifera* (Linnaeus), whose southern terminus is in Pennsylvania, below the Wisconsin drift border;[1] *Alasmidonta marginata* (Say), which is restricted to the upper Susquehanna River, Pennsylvania; and *Anodonta cataracta fragilis* Lamarck from Nova Scotia and northward (figured by Athearn and Clarke, 1962: 28, pl. 2, figs. 3–4, and Clarke and Rick, 1963: 15). Forty species comprise the unionid fauna of the Atlantic Slope region, but one, *Lampsilis ovata* (Say), was artificially introduced from the west at the turn of the century (p. 387). Of the remaining thirty-nine species, sixteen occur in the Northern Atlantic Slope region. Twelve of these are also found in the Southern Atlantic Slope region. Of the twenty-three additional species found on the Southern Atlantic Slope, seven appear to have been derived from the west, nine are endemic to the region, and seven are endemic to individual river systems.

The Atlantic Slope unionid fauna is

[1] Flint (1957: 361) mentioned that along the Atlantic coast, the limit of the Nebraskan drift border extends somewhat farther south of the limit of the Wisconsin drift border (sometimes earlier referred to as the terminal moraine), but that it is ill defined.

TABLE 2, B. UNIONIDAE THOUGHT TO HAVE ORIGINATED ON THE ATLANTIC SLOPE, FOUND IN THE APALACHICOLAN REGION, AND WHICH AFFORD EVIDENCE OF A FORMER CONFLUENCE OF THE APALACHICOLA AND SAVANNAH RIVER SYSTEMS.

	Apalachicola River system	Altamaha River system	Ogeechee River system	Savannah River system	Edisto River system	Cooper-Santee River system	Pedee River system	Waccamaw River system	Cape Fear River system	Neuse River system	Pamlico River system	Roanoke River system	Chowan River system	James River system	York River system	Rappahannock River system	Potomac River system
E. complanata	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×
E. lanceolata	×	×	×	×	×	×		×	×	×	×	×	×	×	×	×	×
A. cataracta cataracta	×	×		×		×	×	×	×	×		×	×	×		×	×
A. couperiana	×	×		×		×			×								

TABLE 2, C. UNIONIDAE DERIVED FROM THE APALACHICOLAN REGION, FOUND IN THE SAVANNAH RIVER SYSTEM, WHICH AFFORD EVIDENCE OF A FORMER CONFLUENCE WITH THE APALACHICOLA RIVER SYSTEM, AND WHICH TERMINATE IN THE SOUTHERN ATLANTIC SLOPE REGION.

	Altamaha River system	Ogeechee River system	Savannah River system	Edisto River system	Cooper-Santee River system	Pedee River system	Waccamaw River system	Cape Fear River system	Neuse River system	Pamlico River system	Roanoke River system	Chowan River system	James River system	York River system	Rappahannock River system	Potomac River system
U. tetralasmus	×	×	×	×	×	×	×	×	×	×	×	×				
A. imbecilis	×	×	×		×	×		×				×				
V. vibex	×	×	×	×	×	×	×	×								
E. icterina	×	×	×	×	×	×	×	×								
E. arctata			×		×			×								
A. triangulata		×	×		×											
E. fraterna			×													

distinct, consisting of species clearly derived from the fauna of the Interior Basin, and a secondary, or Atlantic (Simpson, 1900: 505), fauna also originally of Interior Basin origin, but whose ancestry is more remote. The Atlantic fauna consists of *Elliptio spinosa* (Lea), *Alasmidonta heterodon* (Lea), and *A. undulata* (Say). It may also include *A. triangulata* (Lea) and *Pleurobema collina* (Conrad).

All of these ten species (Table 2, A) are found in the Northern Atlantic Slope region. One of them, *Anodonta implicata*, is not found in the Southern Atlantic Slope region, whereas the remaining nine species terminate there. *A. implicata*, *Lampsilis*

TABLE 2, D. SUMMARY OF THE RELATIONSHIPS OF THE UNIONIDAE OF THE SAVANNAH RIVER SYSTEM. THE ARROWS IN THE FOLLOWING ILLUSTRATION INDICATE THE POSSIBLE DIRECTION OF MIGRATION.

Savannah River system		Apalachicola River system
1. *Pleurobema masoni* (Conrad)	←(1)	*Pleurobema pyriforme* (Lea)
2. *Elliptio congaraea* (Lea)	←(2)	*Elliptio fraterna* (Lea)
3. *Elliptio fraterna* (Lea)	←(3)	*Elliptio fraterna* (Lea)
4. *Elliptio complanata* (Lightfoot)	→(4)	*Elliptio complanata* (Lightfoot)
5. *Elliptio icterina* (Conrad)	←(5)	*Elliptio icterina* (Conrad)
6. *Elliptio arctata* (Conrad)	←(6)	*Elliptio arctata* (Conrad)
7. *Elliptio lanceolata* (Lea)	→(7)	*Elliptio lanceolata* (Lea)
8. *Uniomerus tetralasmus* (Say)	←(8)	*Uniomerus tetralasmus* (Say)
9. *Lasmigona subviridis* (Conrad)		
10. *Alasmidonta triangulata* (Lea)	←(9)	*Alasmidonta triangulata* (Lea)
11. *Alasmidonta varicosa* (Lamarck)		
12. *Anodonta c. cataracta* Say	→(10)	*Anodonta c. cataracta* Say
13. *Anodonta imbecilis* Say	←(11)	*Anodonta imbecilis* Say
14. *Anodonta couperiana* Lea	→(12)	*Anodonta couperiana* Say
15. *Strophitus undulatus* (Say)		
16. *Carunculina pulla* (Conrad)	←(13)	*Carunculina parva* (Barnes)
17. *Villosa vibex* (Conrad)	←(14)	*Villosa vibex* (Conrad)
18. *Villosa delumbis* (Conrad)	←(15)	*Villosa lienosa* (Conrad)
19. *Lampsilis cariosa* (Say)		
20. *Lampsilis ochracea* (Say)		
21. *Lampsilis splendida* (Lea)		

Table 2, E. Unionidae endemic, with an exception, to the Southern Atlantic Slope region.

	Altamaha River system	Ogeechee River system	Savannah River system	Edisto River system	Cooper-Santee River system	Pedee River system	Waccamaw River system	Cape Fear River system	Neuse River system	Pamlico River system	Roanoke River system	Chowan River system	James River system	York River system	Rappahannock River system	Potomac River system
P. masoni		×	×			×		×	×	×	×	×	×			
V. constricta					×			×	×	×	×		×			
P. collina										×			×			
V. delumbis	×	×	×	×	×	×	×	×	×							
C. pulla	×		×		×			×	×							
E. congaraea		×	×	×	×	×		×								
L. splendida	×	×	×		×											
E. dariensis[1]	×															

[1] Also found in the St. Johns River system, Florida.

radiata, Alasmidonta varicosa, L. ochracea, and *L. cariosa* originated on the Northern Atlantic Slope. *Strophitus undulatus* and *Lasmigona subviridis* are thought to have crossed the divide of the Appalachian Mountains. *Ligumia nasuta* probably originated in the lake drainage of Ohio. *Alasmidonta heterodon* and *A. undulata* are probably relicts. The origin of these species are discussed in Chapter 3.

Elliptio complanata and *Anodonta cataracta* are found throughout the Northern Atlantic Slope Region, and probably originated there. *Elliptio lanceolata* extends only to the Susquehanna River system, Pennsylvania, and is thought to be of southern origin. All three of these species (Table 2, B) are discussed (in detail) in Chapter 3. *Anodonta couperiana* is abundant in Peninsular Florida, but since it does not appear to be present in the Suwanee and Withlacoochee river systems, it probably spread into the Apalachicolan region by stream confluence.

In the Apalachicolan region, *E. complanata* is found only within the Apalachicola River system, where it does not reach the size it does on the Atlantic Slope. *E. lanceolata* and *A. cataracta* are more widely distributed than *E. complanata;* but all three species are much less abundant there than they are on the Atlantic Slope.

Seven species of Unionidae (Table 2, C) entered the Southern Atlantic Slope region directly from a former confluence of the headwaters of the Apalachicola and Savannah river systems, and they all reach the limits of their distribution within this region.

Of the twenty-one species of Unionidae found in the Savannah River system, eleven species (Table 2, D) also occur in the Apalachicola River system, and another five were probably derived from Apalachicolan species. The remaining five species are clearly of Atlantic Slope origin.

Seven species of Unionidae are endemic to the Southern Atlantic Slope (Table 2, E) and one other extends into the Atlantic drainage of Peninsular Florida. The following possible species pairs, or analogs, are suggested:

Savannah River system	Apalachicola River system
P. masoni	*P. pyriforme*
E. congaraea	*E. fraterna* or *c. crassidens*
C. pulla	*C. parva*
V. delumbis	*V. lienosa*

Southern Atlantic Slope region	Southern Atlantic Slope region
P. collina	*P. masoni*
E. dariensis	*E. congaraea*
L. splendida	*L. radiata radiata*

Southern Atlantic Slope region	Tennessee River system
V. constricta[1]	*V. vanuxemensis*

[1] Discussed in Chapter 3, p. 280.

Table 2, F. Unionidae endemic to individual river systems of the Southern Atlantic Slope region.

	Altamaha River system	Ogeechee River system	Savannah River system	Edisto River system	Cooper-Santee River system	Pedee River system	Waccamaw River system
E. waccamawensis							×
E. spinosa	×						
E. hopetonensis	×						
E. shepardiana	×						
A. arcula	×						
A. gibbosa	×						
L. dolabraeformis	×						

Seven species of Unionidae are endemic to individual Atlantic Slope river systems (Table 2, F), six of them to the Altamaha. These are discussed below. The species pair *Elliptio waccamawensis—E. congaraea* is recognized.

It is suggested that the species in the left hand list evolved in some part of the Altamaha River system that must have been isolated for considerable time. Text-figure 3 shows that the Hazlehurst Terrace caused the Ocmulgee and Oconee rivers to be separated. This terrace was formerly thought to have been formed during the early Pleistocene, but has recently been dated as Upper Miocene (Alt and Brooks, 1965: 407). If this latter date is correct, this isolation probably bears little or no relevance to the present fauna. (See Table 2, G.)

CHAPTER 3

The Unionacea of the Northern Atlantic Slope region, with a discussion of the probable origin of some of the Atlantic Slope species.

The Northern Atlantic Slope region has already been defined as extending from the York River system, Virginia, to the lower St. Lawrence River system, Canada, and beyond to Newfoundland and Labrador. All of the thirteen species that repopulated the Northern Atlantic Slope at the end of the Pleistocene above the limit of Wisconsin drift (near the Pennsylvania-New York boundary) are found between the York River system and the drift border.

Analysis of the distribution of the species.

Sixteen species comprise the Unionacea of the Northern Atlantic Slope region (Table 3). Eight are considered to be of northern origin (Table 3, A); three are of southern origin; three crossed the divide of the Appalachian Mountains; one is of ancient origin from palearctic Europe; one is of rather recent western origin. Clearly western species found at certain areas of postglacial contact, such as upper New York State and Lake Champlain, but which have

Table 2, G. Relationships of some of the Unionidae of the Altamaha River system.

With the one exception noted above, all of the Unionidae that are endemic to individual river systems in the Southern Atlantic Slope occur in the Altamaha. The following relationships are suggested for some of the species that occur there.

Elliptio spinosa (Lea)	[Not closely related to any other recent species, probably a relict.]
Elliptio dariensis (Lea)	*Elliptio congaraea* (Lea) (Allopatric)
Elliptio hopetonensis (Lea)[1]	*Elliptio complanata* (Lightfoot) (Sympatric)
Elliptio shepardiana (Lea)	*Elliptio lanceolata* (Lea) (Sympatric)
Alasmidonta arcula (Lea)	*Alasmidonta triangulata* (Lea) (Allopatric)
Anodonta gibbosa Say	*Anodonta cataracta cataracta* Say (Sympatric)
Lampsilis dolabraeformis (Lea)	*Lampsilis cariosa* (Say) (Allopatric)
Lampsilis splendida (Lea)[2]	*Lampsilis radiata radiata* Gmelin (Allopatric)

[1] Also found in the St. Johns River system, Florida.
[2] Endemic to the Southern Atlantic Slope.

Table 3. The Unionacea of the Northern Atlantic Slope region.

1. *Margaritifera margaritifera* (Linnaeus)
2. *Elliptio complanata* (Lightfoot)
3. *Elliptio lanceolata* (Lea)
4. *Lasmigona subviridis* (Conrad)
5. *Alasmidonta undulata* (Say)
6. *Alasmidonta marginata* (Say)
7. *Alasmidonta varicosa* (Lamarck)
8. *Alasmidonta heterodon* (Lea)
9. *Anodonta cataracta cataracta* Say
10. *Anodonta cataracta fragilis* Lamarck
11. *Anodonta implicata* Say
12. *Strophitus undulatus* (Say)
13. *Ligumia nasuta* (Say)
14. *Lampsilis cariosa* (Say)
15. *Lampsilis ochracea* (Say)
16. *Lampsilis radiata radiata* (Gmelin)

not spread significantly into the region, are not discussed.

Ortmann (1906, and 1913a: 364) suggested that the ancestors of the Atlantic Slope Unionidae listed above, with the exception of *Elliptio complanata* (Table 3, A), migrated around the northern end of the Appalachian Mountains, in preglacial times, by way of the Eirigan River, which flowed in the direction of the present St. Lawrence River. There was no barrier to their dispersal southward because the base-leveled coastal plain then extended much farther seaward.

During glacial episodes of the Pleistocene, the species found on the eastern side of the mountains were effectively separated from those of the Interior Basin, and speciation took place among them, probably south of the limit of glacial drift, early in the period. Later some of these species spread into the Southern Atlantic Slope region where the coastal region was base-leveled. After the Pleistocene, this assemblage of species occupied most of the northern territory lost by its predecessors.

Ortmann (1913a: 361) was unaware of the complete distribution of *E. complanata* and suggested that it had its center of radiation somewhere on the Southern Atlantic Slope. Matteson (1948a: 131) indicated that the predecessor of *complanata* reached the Savannah River system from the Alabama-Coosa River system by stream capture. In Chapter 1 of this paper, a different order of stream capture is postulated. It appears that the Apalachicola and Savannah river systems were connected and separated before the Apalachicola and Alabama-Coosa were joined, judging from the distributional evidence afforded by the unionid fauna. The present distribution of *complanata* in the Apalachicolan region, as it is restricted to the Apalachicola River system, also indicates this order of stream capture. It was probably already a species before its ancestor, unidentified by Matteson, was supposed to have arrived on the Atlantic Slope. *E. complanata* is related to *dilatata* (figured by Ortmann, 1919: 95, pl. 8, fig. 2) of the Interior Basin. Both species enjoy a certain ubiquitousness within their areas of distribution. The history of *complanata* is, in short, probably similar to that of the other species discussed above.[1]

Table 3, A. Unionidae found in the Northern Atlantic Slope region with close affinities to species of the Interior Basin, believed to have come around the northern end of the Appalachian Mountains.

Interior Basin	Northern Atlantic Slope
E. dilatata	*E. complanata*
A. marginata	*A. varicosa*
A. grandis	*A. cataracta cataracta*
A. grandis	*A. cataracta fragilis*
A. grandis	*A. implicata*
L. ovata	*L. cariosa*
L. ovata	*L. ochracea*
L. radiata siliquoidea	*L. radiata radiata*

[1] Walker (1910: 131) suggested the same origin of *E. complanata* as that presented here. He further thought that *L. subrostrata* and *L. nasuta*, and *A. calceolus* (figured by Clarke and Berg, 1959: 29, fig. 30) and *A. heterodon* had similar relationships and the same origins as the species pairs discussed above. However, Ortmann's arguments as to their origins are thought to be more trenchant and are followed here.

Ortmann (1919: 109) called attention to the presence of *complanata* in the small tributaries of the West Branch of the Susquehanna River, Pennsylvania, close to the divide, and to *dilatata* in the Allegheny River drainage, but he did not suggest that *dilatata* entered the Atlantic Slope here and speciated. He did, however, suggest that *Strophitus undulatus* and *Alasmidonta marginata* entered the Atlantic Slope here. These species are discussed later.

The Margaritiferidae is represented on the Northern Atlantic Slope region by a single species, *Margaritifera margaritifera*. It is a special case because of its origin, but it is included here since its post-glacial history is similar to that of the other species discussed above.

There is good evidence that *M. margaritifera* (figured by Ortmann, 1919: 2, pl. 1, fig. 1) reached the Pacific region from Asia during the Miocene or early Pliocene when the two continents were connected by a North Pacific (Bering) bridge (Walker, 1910). Walker further speculated that this species separately reached the Atlantic Slope by an Atlantic bridge over Iceland and Greenland, probably at roughly the same time.[1]

In any event, *M. margaritifera* appears to have reached eastern North America before the Pleistocene, during which time its range was restricted. Ortmann (1913a: 378) found it in Pennsylvania just south of the limit of glacial drift and suggested that Pennsylvania was at least one refugium where *M. margaritifera* survived the Pleistocene Epoch. Its present distribution, from Pennsylvania to Newfoundland and Labrador, is the result of a reoccupation of territory. Besides differing anatomically, this species contrasts with the Unionidae in its ecological preferences, since it lives in cold water of high alkalinity.

[1] The North Pacific bridge is well established. Kurtén (1966: 4) believes there were three separate intermigrations by this route, one in the late Paleocene, another in the early Eocene, and a third at some time in the late Middle or beginning of the late Upper Eocene. He further suggests a North Atlantic connection including the British Isles, Iceland, and Greenland, in the late Paleocene and early Eocene.

Table 3, B. Unionidae found in the Atlantic Slope region which appear to have crossed the divide of the Allegheny Mountains, or are represented by allopatric species.

Interior Basin	Atlantic Slope region
L. subviridis	*L. subviridis*
V. vanuxemensis	*V. constricta*
Allegheny River drainage	Upper Susquehanna River drainage
A. marginata	*A. marginata*
S. undulatus	*S. undulatus*

Ortmann (1913a: 371) found *Lasmigona subviridis* to be the dominant species in the Greenbrier and New rivers of the Kanawha River system, which extends across the divide but drains on the western side of it. With the exception of this one western drainage, the species is limited to, and rather widely distributed on, the Atlantic Slope. He suggested that this species developed in the western mountain streams from *Lasmigona compressa* (Lea) (figured by Clarke and Berg, 1959: 31, fig. 29), with which it appears to be allopatric; though, at present, the range of *compressa* is not close to that of *subviridis*. It lives in small creeks where the best opportunities for fishes to cross from one river system to another develop. Ortmann thought that it spread into the Atlantic Slope region by way of stream capture with the upper James River, but it has since been reported from the Roanoke River system, permitting the assumption that it might have reached the Atlantic Slope by stream capture between the New and Roanoke rivers. (See p. 285.)

Villosa constricta is restricted to the Southern Atlantic Slope, between the upper Catawba River of the Cooper-Santee River system and the James River system. It is

very close to *Villosa vanuxemensis* (Lea), (for reference to a figure see Simpson 1914, 1: 165) which is found in the Holston River and elsewhere in the Tennessee River system. It is not obvious where the ancestor of *constricta* came from; it may have entered the Roanoke from the New River along with *L. subviridis*, if it can be assumed that *vanuxemensis* was more widely distributed in pre-glacial time.

Strophitus undulatus and *Alasmidonta marginata* crossed the divide in central Pennsylvania, in the vicinity of Cambria, Westmoreland, and Indiana counties, where the Susquehanna drainage of the east has largely encroached on the Allegheny River of the west, and where stream capture has taken place (Ortmann, 1913a: 368). *A. marginata* remained restricted to the upper Susquehanna River system, while S. *undulatus* spread throughout the Atlantic Slope region. Both of these species go into very small streams and, in general, avoid large rivers.

Ligumia nasuta is allopatric with *L. subrostrata* Say (for reference to a figure see Simpson, 1914, 1: 99) of the central and western part of the Interior Basin. It probably developed in the lake drainage of Ohio in postglacial time and spread eastward into the Hudson River, following a course along the baseleveled coastal plain. It reached the James River system in the south and the St. Lawrence River system, Canada, in the north (Ortmann 1913a: 379). This species has a preference for quiet water.

Elliptio lanceolata occurs in the Apalachicolan region and on the Atlantic Slope but there it extends only to the Susquehanna River system, Pennsylvania. The present distribution argues that this is a southern species, but its immediate ancestors or the area of its speciation is obscure.

Alasmidonta undulata and *Alasmidonta heterodon* appear to be relicts of a much older, westerly derived fauna, since they no longer closely resemble any of the members of the genus found in the Interior Basin, nor do they resemble one another. These two *Alasmidonta* appear to have long existed on the Southern Atlantic Slope, but are now widely distributed above the drift border.

CHAPTER 4

The generic affinities of the Unionacea of the Apalachicolan region, Peninsular Florida, and Southern and Northern Atlantic Slope regions.

Summary

Over forty genera of Unionidae occur in the Interior Basin, many of which are also found in the Alabama-Coosa River system. In the Apalachicolan region are fourteen genera that occur in the Interior Basin as well as in the Alabama-Coosa River system. An additional genus, *Glebula*, is limited to the Coastal regions. In the Apalachicolan region also occur *Margaritifera*, *Alasmidonta s. s.*, and *Quincuncina*. The latter is endemic. The six genera found in Peninsular Florida occur in both the Apalachicolan and Atlantic Slope regions but are probably derived mostly from the former.

Nine of the eleven genera of Unionidae found in the Southern Atlantic Slope region are found in the Apalachicolan region. The exceptions are *Lasmigona* and *Ligumia*. Four of the genera appear to be of southern origin, and the remainder have affinities with both the north and south. Only seven of these genera occur in the North Atlantic Slope region. This region is also occupied by *Margaritifera*, which does not occur on the Southern Atlantic Slope.

Ortmann (1913a: 323), speaking of the Unionidae that reached the Atlantic Slope around the northern end of the Appalachian Mountains, noticed the diminution of genera from the Interior Basin, and concluded that "the Allegheny Mountains formed an important barrier to the eastward distribution of the bulk of the western fauna." It is noted here that along the

Table 4, A. The genera of Unionacea in the Apalachicolan region.

Margaritifera[1]	*Anodontoides*
Fusconaia	*Strophitus*
Ambelma[2]	*Obovaria*[4]
Quincuncina	*Carunculina*
Pleurobema	*Villosa*
Elliptio	*Lampsilis*
Uniomerus	*Medionidus*
Alasmidonta[3]	*Glebula*
Anodonta	

[1] See note on p. 280.
[2] See note on p. 270.
[3] *Alasmidonta* is represented in the Alabama-Coosa River system by *A. mccordi* Athearn (1964: 134, pl. 9, figs. a, b).
[4] *Obovaria* is found in the Alabama-Coosa River system and is represented in the Apalachicolan region only in the Escambia River, the next system immediately east of the Alabama-Coosa River system.

southern coastal plain, where no such great barrier existed, there is a similar diminution of genera from west to east.

It can be seen in Table 1 that fifteen of the seventeen genera found in the Apalachicolan region (Table 4, A) occur in the Alabama-Coosa River system. The exceptions are *Margaritifera* (represented by *M. hembeli*, a relict), which is also found in one other drainage to the west, the Bayou Teche, Louisiana, and *Quincuncina*, which is endemic to the Apalachicolan region. Although *Alasmidonta* occurs in the Alabama-Coosa River system, it does not appear close to *Alasmidonta s. s.*, which is found only in the Apalachicolan and Atlantic Slope regions.

Peninsular Florida is considered to be the area south and east of the Suwannee River system and south of the St. Marys River system. (Both of these systems are included here in the Apalachicolan region.) In this area occur only six genera (Table 4, B) derived from the west and north-east.

Table 4, B. The genera and subgenera of Unionidae in Peninsular Florida.

Elliptio s.s.
Uniomerus
Anodonta s.s [Not represented in this area]
Utterbackia
Carunculina
Villosa
Lampsilis s.s

Table 4, C. The genera and subgenera of Unionidae in the Southern Atlantic Slope region.

Pleurobema s.s. [Not represented in this area]
Lexingtonia. Endemic to the Southern Atlantic Slope
Elliptio s.s.
Cauthyria. Endemic to the Altamaha River system
Uniomerus
Lasmigona s.s [Not represented in this area]
Platynaias
Alasmidonta s.s.
Prolasmidonta. Endemic to the entire Atlantic Slope
Decurambis
Anodonta s.s. [Not represented in this area]
Pyganodon
Utterbackia
Strophitus
Carunculina
Villosa
Ligumia
Lampsilis s.s.

Of the eleven genera (Table 4, C) found in the Southern Atlantic Slope region, nine are represented in the Apalachicolan region where there is a total of seventeen genera. *Strophitus*, *Lasmigona*, and *Ligumia* are clearly from the North. Of these, *Strophitus* alone is represented in the Apalachicolan region by *S. subvexus* (Conrad), which is endemic to the region.

Of clearly southern origin are *Uniomerus* and *Carunculina*. *Pleurobema* and *Villosa* are probably of southern origin. The genera *Elliptio*, *Alasmidonta*, *Anodonta*, and *Lampsilis* have affinities with both the southern and northern elements of the fauna.

Of the eleven genera (Table 4, D) found in the Southern Atlantic Slope region, seven occur in the Northern Atlantic Slope region, where there also occurs an additional genus of Unionacea, *Margaritifera*. These eight genera repopulated the entire Northern Atlantic Slope above the limit of glacial

Table 4, D. The genera and subgenera of Unionacea in the Northern Atlantic Slope region.

Margaritifera
Elliptio s.s
Lasmigona s.s
Platynaias
Alasmidonta s.s.
Prolasmidonta. Endemic to the Atlantic Slope region
Decurambis
Anodonta s.s. [Not represented in this area]
Pyganodon
Strophitus
Ligumia
Lampsilis s.s.

drift, with the exception of *Lasmigona*, which only reaches the Hudson River system, New York. One of these, *Ligumia*, appears to have entered from the west at the close of the Pleistocene. With this exception, the other genera were established below the limit of glacial drift before that period.

CHAPTER 5

The relationship of the geomorphology and topography of the Apalachicolan and Atlantic Slope regions to their unionid faunas.

The Appalachian Mountains have been an effective barrier to the spread of Unionacea from the Interior Basin to the coastal area since postcretaceous time (Ortmann, 1913a: 383), although the original Appalachian Mountains were formed much earlier in the Permian Period as the result of lateral pressure. They consisted of a number of parallel anticlines and synclines that ran in a northeast-southwestern direction. These folds were pressed against an old block of Archaic rocks, the present Piedmont Plateau, that lay to the east of them.

The highest elevation of these folds was in the south, and the divide was well to the east, close to the old Archaic land. The rivers followed the structure of the mountains, running first between the parallel ridges (anticlines) in the synclinal valleys, and finding their outlets in a northwesterly direction toward the Interior Basin. On the Atlantic side of the divide, shorter streams originated in the highest elevations and flowed east and southeast across the Archaic rocks. Rivers also formed on the tops of the anticlines, and anticlinal valleys developed, parallel to the synclinal ones. The uppermost rocks of the anticlines were largely hard sandstones of Carboniferous age, below which were softer shales and limestones of Devonian age or older. The synclinal rivers ran uniformly over the same hard sandstone, but the anticlinal rivers, primarily those on the highest elevations, were the first to cut through the sandstone, allowing the rivers access to the softer rocks below. In time, the anticlinal valleys became more excavated than the synclinal valleys. This process advanced farthest in the eastern section of the mountains, so that what was once the highest elevation became a deep valley.

By the Cretaceous Period, nearly all of the Appalachian area was peneplaned, with the exception of a chain of monadnocks between eastern Tennessee and North Carolina, and scattered hills in northern New England. (These unreduced areas form the modern Great Smoky Mountains and the summits of the White Mountains in New Hampshire. Elsewhere there are widespread remnants of the peneplane even on the crests of the highest present ridges.) The coastal plain was covered with a shallow sea that deposited a veneer of beds on the Archaic rocks. Because of certain characteristics of the patterns of some of the present streams, it is thought that this sea extended further inland than is now indicated by existing beds.

The relief of the present Appalachian Mountains is due almost wholly to a series of broad regional upwarps that occurred in the early Cenozoic Era, giving the present elevation both to the already extant

mountain structures and to the subsequent sculpture of this complex mass by erosion. The Appalachian Mountain system of eastern North America extends in a wide belt, more or less parallel to the coast line for more than 1600 miles from the Gulf Coastal Plain in central Alabama to the St. Lawrence River, Quebec. The mountains are divided from west to east into four provinces. 1) The Cumberland, or Appalachian Plateau, which extends from Alabama to New York and merges with the Allegheny Plateau. This western area has been peneplaned, but the soft rocks of pre-Carboniferous age have not been reached. 2) The Appalachian Valley and Ridges that reach from Alabama to New York. In the south, this province has a valley-like appearance, but in the north, it becomes the Allegheny Mountains. The eastern part of these were originally much higher. They are cut into by anticlinal streams, which have carved out broad limestone valleys, with high ridges of harder rock between them. Within the Allegheny Mountains, and parallel to them on the east, where there was once the highest elevation, there is now the exceptionally broad Great Allegheny Valley. 3) The Blue Ridge is the highest part of the Southern Appalachian Mountains and extends from northeastern Georgia across western South and North Carolina into southwestern Virginia. The Blue Ridge of the Central Appalachians extends from Central Virginia into Pennsylvania where it continues as South Mountain. It is the flank of an anticline, consisting largely of Archaic rocks. It is less elevated here than in the south. 4) The Piedmont Plateau (or Upland) goes from central Alabama to the Hudson River, New York.

To the east of these mountain provinces lies the Coastal Plain; this is a continuation of the Archaic granites of the Piedmont Plateau, over which are much younger Cretaceous and Tertiary deposits of sea-lain limestone and poorly consolidated sand and clay. Waterfalls are so numerous at the boundary between the Piedmont Plateau and the Coastal Plain that it is known as the Fall Line. During the Pleistocene, a number of changes in the level of the ocean left terraces on the Coastal Plain that will be discussed below.

The whole Appalachian Mountain system has also been divided from south to north into three regions. 1) *Southern.* Northeastern Georgia to the New or Kanawha River, Virginia, and West Virginia. 2) *Central.* New River to the Hudson River valley (covered here to the Potomac River system). 3) *Northern.* Hudson River valley to the lower St. Lawrence River. This adumbration of the complex history of the Appalachian Mountains, primarily of the area under study, is offered as background. The relevant details follow.

The main backbone of the present Appalachian Mountains extends continuously from the divide between the Toccoa and Coosawattee rivers in northeastern Georgia to northern Virginia, and is known as the Blue Ridge. From it the streams flow northwest, southeast, or east. It has been mentioned that the original divide was well to the east, as is the present divide, and that the eastern streams did, and do, have a steeper grade and a shorter, more direct route to the sea. Since they had, and have, more eroding power than the streams of the western drainage, they have encroached on it. There has also been a tendency of the rivers on the Atlantic Slope to capture streams between systems.

Evidence of stream capture. The southern extremity of the Blue Ridge is the watershed of a number of rivers. The Toccoa, the Little Tennessee, and the French Broad all flow into the Interior Basin. Of concern here are the two systems that originate on the southeast side of the mountains and that flow into the Gulf of Mexico; the Etowah River of the Alabama-Coosa River system, which flows westward around Pine Mountain, Georgia, into the Appalachian

Valley and then into the Gulf; the Chattahoochee River of the Apalachicola River system, which flows southwestward into the Gulf; and the Tugaloo River of the Savannah River system, which also heads in the mountains and flows southeast into the Atlantic Ocean. On the Piedmont Plateau, as can be seen in Text-figure 1, (see p. 268) all three of these rivers have tributaries that presently are separated by minor divides. Matteson (1948a: 131) suggested that confluence occurred among these streams during the late Tertiary. It may have been later, but in any event, the distribution of the Unionidae in the several river systems indicates that confluence did take place.

A number of other Atlantic Slope river systems, in addition to the Savannah, have their sources near or in the Blue Ridge. The Cooper-Santee River system, which drains some 15,000 square miles of central South Carolina, has three main tributaries, the Saluda, Broad, and Catawba, all of which originate close to the divide. The Pedee River system's main tributary, the Yadkin, begins in Watauga and Caldwell counties, North Carolina, near the divide. The Roanoke River system, which has the Dan River as a major tributary, forms in Patrick County, Virginia. The Roanoke itself commences in the eastern foothills of the Blue Ridge.

It is only in the southern Appalachians that streams that flow westward still have their sources near, or in, the Blue Ridge. The best example is the New River, which preserves its ancient course and cuts across the divide. According to Campbell (1896: 674) there is a good example of stream capture in the uppermost Roanoke River, Virginia (Plate 1).

The headwaters of the Roanoke's North Fork run first in a southwesterly direction in a valley that clearly continued to New River; but just north of Christiansburg, Montgomery County, Virginia, the North Fork makes a sharp bend, cuts through Paris Mountain, then flows eastward and northeastward. It is clear that the Roanoke River has captured here a tributary of the New River. The presence of *Lasmigona subviridis* and *Villosa constricta* in the Atlantic Slope region adds credence to the geomorphological evidence.

Beginning with the Roanoke, the succeeding river systems, the James, Potomac, and Susquehanna, all flow more directly east and each one cuts farther back into the mountains (Campbell, 1896: 675). Campbell also assumes that stream capture has taken place between the headwaters of the Roanoke and James river systems, an assumption which might explain the presence of *Villosa constricta* in both systems.

The Potomac River cuts across the mountains and has, in northeastern West Virginia, reached the Allegheny Plateau. It now drains a longitudinal synclinal valley. Campbell (1896) further states that in the mountains, the Potomac River robbed the James River of tributaries, and that the Susquehanna River of Pennsylvania encroached on the Potomac. However, these sequences of stream captures seem too ancient to be relevant to the present unionid fauna north of the James. Many of the Unionidae appear to have spread along the baseleveled coastal plain; this spreading is discussed below.

The Piedmont Plateau. In Alabama, the Piedmont Plateau is divided into two regions. 1. The Ashland Plateau, the highest division, is an area of crystalline rocks, diversified by ridges. It is the mountainous portion of the Piedmont and includes Cheaha Mountain, the highest point in the state. It is drained by portions of the Alabama-Coosa River system. 2. The Opelika Plateau is lower and is underlain by Archean rocks; it has no striking topographic features. It is drained by the tributaries of the Tallapoosa River of the Alabama-Coosa system, which lies adjacent to the northwest border of the Archaic

rocks, and by the Chattahoochee River, which forms the eastern boundary of the state. On the Opelika Plateau the rivers have cut valleys some 200 feet below the general surface. The region continues into Georgia as the Greenville Plateau, and is drained by longitudinal streams that flow southwestward and westward to the Gulf. The remaining portion of the Piedmont of Georgia to the north is drained by dendritic streams. Those rivers that originate in the Piedmont of Georgia include: the Flint of the Apalachicola system, which flows into the Gulf, and the Ocmulgee and Oconnee of the Altamaha system and the Ogeechee system, which both flow into the Atlantic. In South Carolina the rivers have their sources in the mountains or on the Coastal Plain. In North Carolina the Piedmont rivers include: the Cape Fear, Neuse, Pamlico, and Chowan systems; and in Virginia, the York and Rappahannock systems.

Ortmann (1913a: 340) observed, in the area he studied, that the great majority of Atlantic Slope Unionidae go up into the mountains (where the rivers may have reached Cretaceous limestone) and approach the headwaters without significant depauperation.

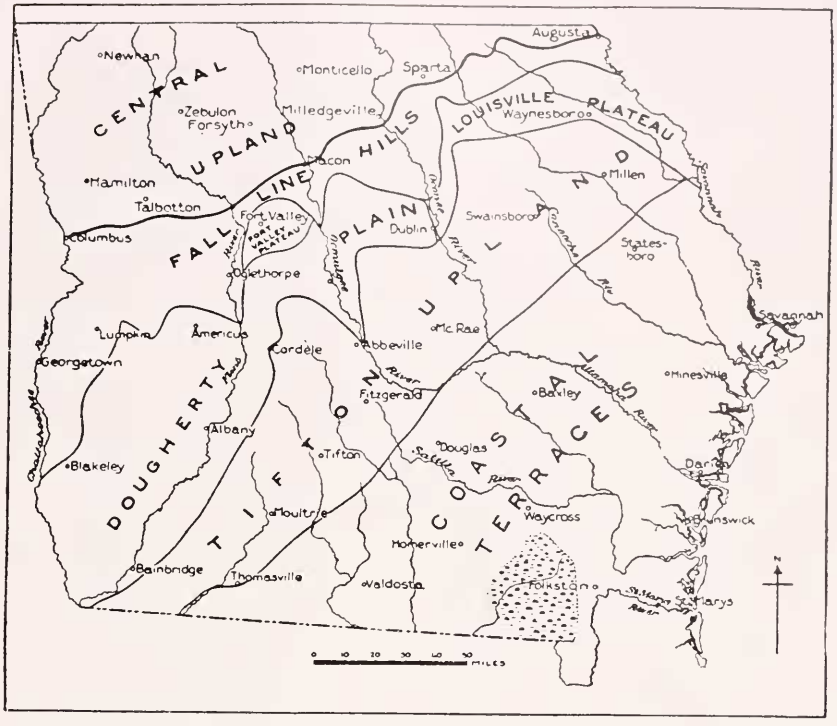
In the Apalachicola River system, present pollution prevents verification, but older records indicate that some of the unionid fauna of the Chattahoochee River extended on the Piedmont at least to the vicinity of Atlanta, Georgia. In the Flint River, which forms south of Atlanta, Unionidae are found in Line Creek, close to the headwaters.

On the Atlantic Slope of Georgia the unionid faunas of the major river systems —the Altamaha, Ogeechee, and Savannah —end abruptly at the Fall Line. The exceptions in the Altamaha River system are *Elliptio complanata* and *Anodonta c. cataracta*, which have been found near Stone Mountain, DeKalb County, the headwaters of the Ocmulgee River. In the Savannah River system the exceptions are *Elliptio complanata*, *E. congaraea*, and *Villosa delumbis*, which are found in the Broad River, opposite to which, in Abbeville County, South Carolina, have also been found *Pleurobema masoni*, *Elliptio fraterna*, *E. arctata*, *Lasmigona subviridis*, and *Lampsilis cariosa*.

The siliceous character of the Piedmont water, as illustrated in Text-figure 4, might offer an adequate explanation for the diminution of the fauna above the Fall Line. However, elsewhere on the Atlantic Slope siliceous water does not appear to be such an inhibiting factor to the distribution of the Piedmont Unionidae.

The Coastal Plain. The Coastal Plain is a continuation of the Archean rocks of the Piedmont over which occur Cretaceous and Tertiary deposits of sea-lain limestone and poorly consolidated sand and clay (Text-fig. 2). In spite of the apparent propinquity of the Apalachicola and Altamaha river systems in the Piedmont where the Chattahoochee passes close by the source of the Ocmulgee, the unionid fauna does not indicate any direct exchange of species. The Flint River has no large tributaries to the east, and in some places it is as much as fifteen miles from the divide that separates it from the drainage to the east, though Big Indian Creek, near Fort Valley, Houston County, a tributary of the Ocmulgee River, is only three miles distant. It would appear that the height of the Tifton Upland and Fort Valley Plateau, and the depth of the river channel on the Dougherty Plain, have prevented stream capture between these river systems for a long time.

During the Pleistocene the Coastal Plain was subjected to a number of invasions by the sea. According to Cooke (1945: 248), the maximum and earliest flooding left a record, the Brandywine Terrace [Hazlehurst in Georgia], which correlates with the Aftonian interglacial stage. The sea was thought to be 270 feet above the present level. As mentioned on p. 268, MacNeil cast doubt on the extent of Afonian flood-



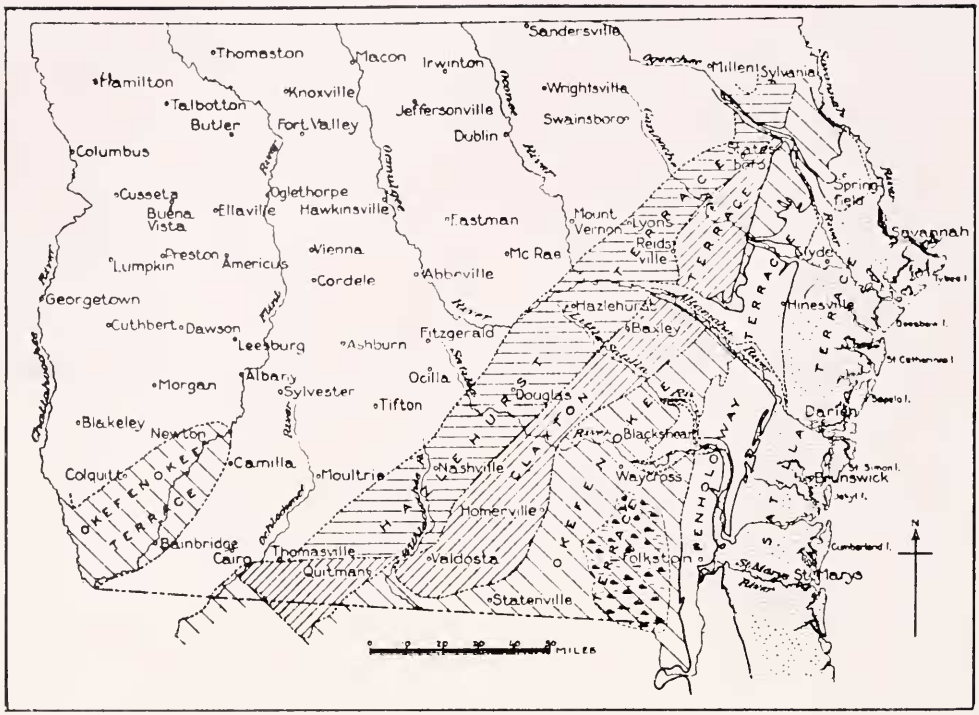
Text-figure 2. The topographic divisions of the Coastal Plain of Georgia. (From La Forge, 1925, fig. 2.)

ing, and concluded that there is no evidence to indicate that the sea ever reached a level more than 150 feet above the present one during the Yarmouth interglacial stage. He regarded the Brandywine Terrace to be of subaerial origin. Russell (1957: 427–428) suggested that the shore lines might have been subjected to differential uplifting.

Oaks and Coch (1963), on the basis of cores made in Virginia, postulated six cycles of the Pleistocene seas, with maximum heights of 45 feet above present levels. They disagreed with the theory of "terrace-stratigraphy" and disapproved of the nomenclature of the terraces, or shore lines.

Alt and Brooks (1965) also objected to the nomenclature of the shore line scarps and their associated terraces, since the implication is that they refer to independent physiographic units rather than to component parts of a single physiographic unit. In spite of these valid objections, some of the terrace names are well established in the literature and are retained here, but are used in the broader sense implied by Alt and Brooks.

On the basis of the geological evidence, Alt and Brooks (1965) concluded that the 215–250 [270] foot shore line was occupied during the Upper Miocene. This dating was confirmed by Laesse (1968) with botanical evidence. Alt and Brooks also concluded that the 90–100 foot shore line was occupied during the Pliocene. Alt (1968) further concluded that the 70–80 foot shore line also dated from the Pliocene. He recognized three Pleistocene shore lines: one at 40–45 feet, which he assigned to the Aftonian interglacial; a second at 25–30 feet, which he assigned to the longer Yarmouth interglacial; and a third at 5–10 feet, which he assigned to the Sangamon interglacial.

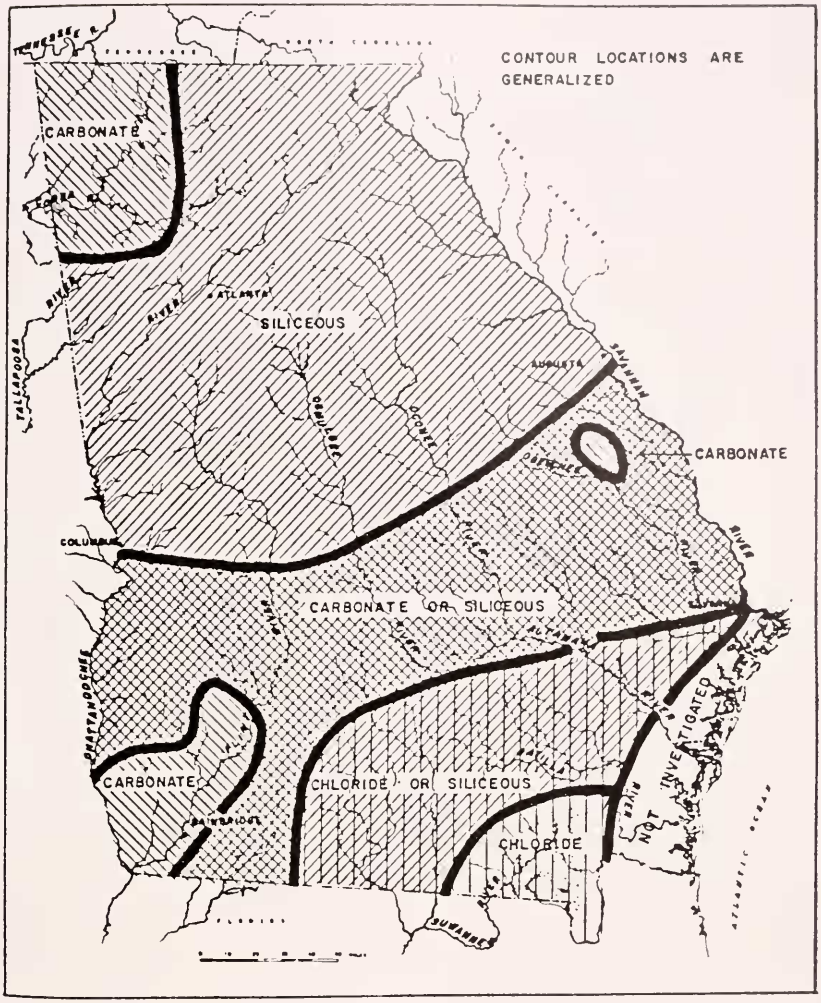


Text-figure 3. The Coastal Terraces on the Coastal Plain of Georgia. (From Cooke, 1925, pl. 10, fig. A.)

The coastal terraces of Georgia are shown in detail in Text-figure 3 because some are especially relevant. These terraces were formerly defined as sea bottom uncovered and converted into land by a drop in sea level, but Hoyt and Hails (1967) now regard these Georgia terraces as former lagoon salt marshes. The terraces are not entirely confined to the coastal region, since all of the larger rivers have terraces of their own. A river terrace may be defined as the old floor of a valley within which an inner valley has been cut by a stream when deepening its channel. Thus, river terraces are fossil flood plains.

The various coastal terraces (or shore lines) are correlated below from oldest (top) to youngest:

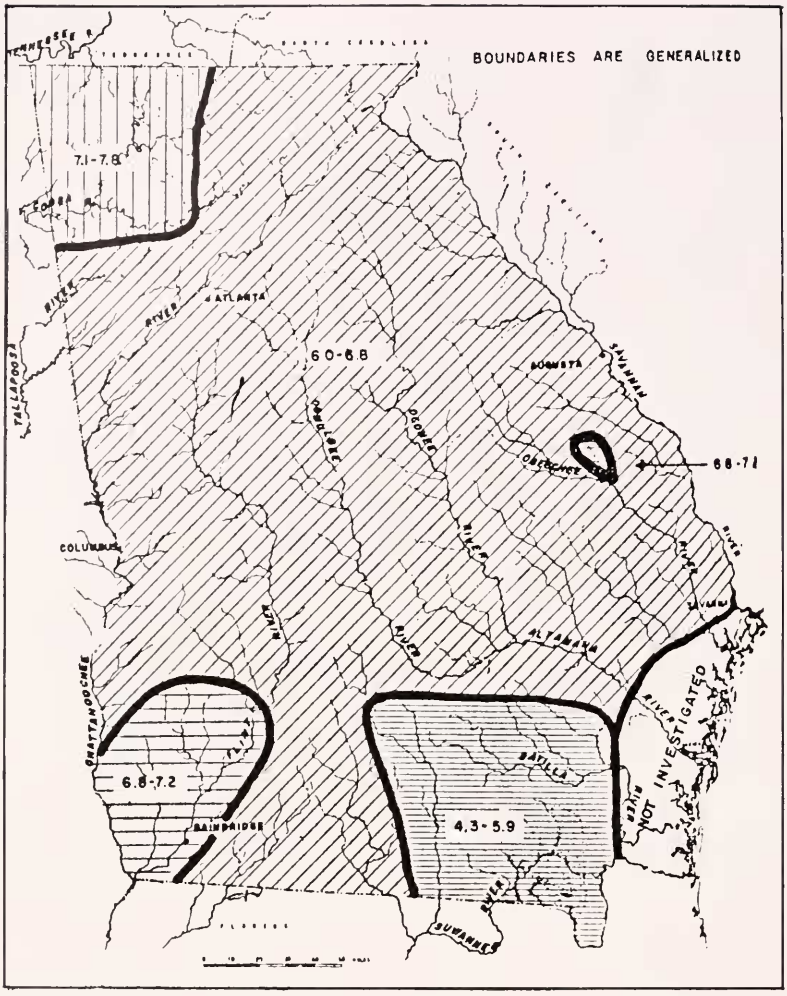
Murray (1961: 508)		Cooke (1925: 35)		MacNeil (1950: 99)	Alt and Brooks (1965) and Alt (1968)	
General maximum height		Georgia	Range	Florida	Time or Stage	
Brandywine	272 feet	Hazlehurst	270–215 feet		Upper Miocene	250–215 feet
Coharie	215 "	Claxton	215–160	Okefenokee	Pliocene	100– 90
Sunderland	170 "	Okefenokee	160–100			
Wicomico	100 "	Penholoway	100–60			
Penholoway	70 "	"		Wicomico	Late Pliocene	80– 70
Talbot	42 "	Satilla	60–0		Aftonian interglacial	50– 45
Pamlico	25 "	"		Pamlico	Yarmouth interglacial	30– 25
					Sangamon interglacial	10– 5



Text-figure 4. Water types of Georgia. (From Cherry, 1961, fig. 6.)

A number of the Coastal Plain rivers appear to have their sources above the level of maximum flooding by the sea; among these are the Escambia, Yellow, Choctawhatchee, Ochlockonee and Suwanee river systems in the Apalachicolan region and the Satilla and Edisto river systems on the Atlantic Slope. The Yellow, Satilla, and Edisto river systems appear to have been more effectively inundated by the sea, because their small unionid faunas suggest subsequent repopulation.

Among the river systems that are completely on that part of the coastal plain that was flooded during the Pliocene is the St. Marys. Text-figure 3 shows that it is entirely on the Okefenokee and Penholoway (Wicomico) formations. The river drains the Okefenokee Swamp, and its water, with a low *p*H, is high in chlorides or silicates (Text-figs. 4 and 5). Although the Satilla River is similar, it differs from the St. Marys in that a small portion of its headwaters is on the Tifton Upland, be-



Text-figure 5. Ranges in pH of Georgia water. (From Cherry, 1961, fig. 8.)

yond the area of maximum Pliocene and Pleistocene flooding. Both rivers have a small unionid fauna (Table 1). The dominant species in the St. Marys is *E. c. crassidens*, and in the Satilla, it is *E. crassidens downiei*. If the Satilla was a refugium, it is possible that *downiei* had a chance to evolve there and that *E. c. crassidens* came back from the west by a route not explained here.

The Waccamaw River system in South and North Carolina is of the same origin as the St. Marys. It is completely on the Wicomico and Chowan formations and has a typical coastal assemblage of Unionidae (Table 2), but it is remarkable in having an endemic species, *E. waccamawensis*.

Among the small river systems of more recent origin on the Coastal Plain in the Apalachicolan region in which Unionidae have been found are the Econfina and the Wasassasa. In the Econfina occur *Elliptio icterina*, *Villosa lienosa*, *V. vibex*, and

Lampsilis anodontoides. *E. icterina* occurs in the Wasassasa.

The systems of more recent origin on the Coastal Plain in the Atlantic Slope region are the Combahee, Ashley, Black, and White Oak rivers. The Combahee has five species: *E. complanata*, *E. icterina*, *Uniomerus tetralasmus*, *V. delumbis*, and *V. vibex*. In the other river systems occur either, or both, *E. complanata* and *icterina*, with the exception of the Black, in which *U. tetralasmus* also occurs.

It is generally regarded that the Pleistocene lasted for a million years, although Flint (1957: 301) states that, "all we can say with confidence is that the last major glaciation occurred within 30,000 years, and on the basis of sea floor stratigraphy, the Pleistocene as a whole, embraces at least 300,000 years, perhaps much more." In any event, during the Pleistocene at least five ice sheets pushed southward into the United States from centers of accumulation in Canada. The interglacial times are thought to have been of long duration with sea levels high. During the shorter glacial times the sea must have been relatively low, and the coastal plain often extended much farther to the east than it does at present.

Emery (1967) has convincingly shown that as early as 19,000 years ago (lowest level of the sea during the Wisconsin glacial stage) that this was so then.

Ortmann (1913a: 383) pointed out that there is a dispersal line directed both north and south on the Coastal Plain, because geophysical barriers have been largely removed by baseleveling. Lowland flooding allows fishes to migrate from one system to another. The present paucity of Unionidae in most of the coastal streams of recent origin indicates that dispersal was probably easier during one of the inter-glacial periods.

The importance of baseleveling and its faunal significance was well illustrated by Adams (1901).

CHAPTER 6

Summary and Conclusions

The Apalachicolan region as defined herein includes not only those river systems flowing into the Gulf of Mexico, from the Escambia to the Suwannee, but also the St. Marys and Satilla, which flow into the Atlantic Ocean. Forty-nine species comprise the unionid fauna of this region. Nineteen have affinities with species to the west or Interior Basin, twelve are endemic to the region, and eleven are restricted to individual river systems. Three species that were probably originally endemic to the region have spread into the Atlantic Slope region, and four others probably originated on the Atlantic slope.

The Atlantic Slope region is defined as those streams flowing into the Atlantic Ocean from the Altamaha River system, Georgia, to the lower St. Lawrence River system, Canada, including rivers in Newfoundland and Labrador. Since the area is occupied by an assemblage of species of both southern and northern origin, it can be divided into Southern and Northern regions. The former extends north to the James River system, Virginia, the northernmost system with a clearly southern assemblage of species. Forty species comprise the unionid fauna of the Atlantic Slope region, but one, *Lampsilis ovata* (Say), was artificially introduced from the west at the turn of the century. Of the remaining thirty-nine species, sixteen occur in the Northern Atlantic Slope region. Of the twenty-three additional species found on the Southern Atlantic Slope, seven appear to have been derived from the west, seven are endemic to the region, and seven are endemic to individual river systems. Two other species, thought to have originated on the Southern Atlantic Slope, are found in Peninsular Florida, and one of them has spread into the Apalachicolan region.

1. Because of their unique mode of distribution, the Unionidae are able to furnish

important evidence for past conditions of drainage by their present distribution, as was demonstrated by Ortmann (1913a: 381). The discontinuous distribution of the Unionidae of the Apalachicolan region indicates that there was once a confluence of the headwaters of the Alabama-Coosa and Apalachicola river systems. The presence of the same species and analogs in the Savannah River system on the Atlantic Slope as in the Apalachicola River also indicates confluence. The absence of some of the species found in both the Alabama-Coosa and Apalachicola river systems indicates that the confluence of the Apalachicola and Savannah river systems took place first. Two minor confluences are postulated: One between Uphauppee Creek of the Alabama-Coosa River system and Uchee Creek of the Apalachicola River system, the other between the headwaters of the Choctawhatchee River system and a tributary of the Chattahoochee River of the Apalachicola River system.

2. Contained in the fauna of the Apalachicolan region are species that are found in the Alabama-Coosa River system, having entered this system through a former confluence with it and the Tennessee River system. The region contains mainly endemic species of Interior Basin origin. A few species have reached it from the Atlantic Slope Region.

3. The presence of endemic species, primarily in the larger Apalachicolan river systems, indicates that these species had refugia above the maximum Pliocene and Pleistocene flooding, and originated before then.

4. Ortmann (1913a: 385) pointed out that the Allegheny Mountains formed an old and well-marked boundary between aquatic animals of the Interior Basin and those of the Atlantic Slope region since post-Cretaceous time. For the Unionidae this boundary includes the entire Appalachian Mountain system.

5. The Atlantic Slope unionid fauna is distinct, consisting of species clearly derived from the fauna of the Interior Basin, and a secondary, or Atlantic fauna (Simpson, 1900: 505), originally of Interior Basin origin, but whose ancestry is more remote.

6. In the Atlantic Slope region, most of the species that are clearly of Interior Basin origin are a northern group that migrated around the northern end of the Appalachian Mountains before the Pleistocene; there is also a southern group that entered the Atlantic Slope region through a confluence of the Apalachicola and Savannah river systems, also in pre-Pleistocene time.

7. The large number of endemic unionids in the Altamaha River system, Georgia, of both old Atlantic and Northern Atlantic Slope origin suggests that this system is particularly old and that it was sufficiently isolated during some of the Pleistocene to have facilitated speciation.

8. Dispersal in the Apalachicolan region appears to have been largely by stream capture. On the Atlantic Slope there is a dispersal line, directed both north and south, where barriers are rendered ineffective by baseleveling (Adams, 1901). The rate of dispersal was undoubtedly influenced by changes in sea level during the Pleistocene. Although it cannot be specifically demonstrated, stream confluence in the uplands also may have played a part in the dispersal of the Atlantic Slope species.

9. In the Appalachian Mountains, there are a few examples of species crossing the divide by stream capture. In addition to the confluence of the Apalachicola and Savannah River systems, there were confluences of the headwaters of the Roanoke and New rivers and of the Allegheny and Susquehanna river systems. Evidence of the former existence of these confluences is borne out by the present distribution of some unionid species in the adjoining systems and by the physiography.

10. *Margaritifera margaritifera* (Linnaeus), an ancient species from Europe,

had a refugium in Pennsylvania below maximum Pleistocene glaciation, and *Ligumia nasuta* (Say) appears to have migrated from the St. Lawrence Basin to the Atlantic Slope in postglacial time. These are two special cases of distribution.

PART II. A REVISION OF THE UNIONIDAE FROM THE ST. MARYS RIVER, FLORIDA, TO THE POTOMAC RIVER, MARYLAND.

INTRODUCTION

In spite of the parochial title of this section, I hold the belief, as do many evolutionary biologists, that most faunal studies are an anathema. Their authors seldom accurately determine subspecies (Mayr, et al., 1953: 181) and often even their determination of species is suspect. My excuse for this faunal approach is thought to be justified by the findings presented in Part I. I have studied the superfamily Unionacea for almost thirty years and each of the forty species covered in this section has been completely monographed, including those whose range extends beyond the area studied. Although the synonymy of each species is believed to be complete, and the modern species concept has been assiduously applied, infallibility of judgment is not claimed. If I am guilty of creating composite species, they will probably be found among the ubiquitous *Elliptio*. Nevertheless, if this is so, the postulations in Part I should not require serious modification since most of the species on which they are based are old and sufficiently discrete to satisfy a typologist.

History of the taxonomists and the collectors of the Atlantic Slope Unionacea.

The Taxonomists

Three species of Unionacea found in the Atlantic Slope region were figured in the first printed book devoted entirely to the study of mollusks. This was the great folio volume by Martin Lister, *Synopsis Methodicae Conchyliorum*, which appeared in London in 1685, at the close of the English Renaissance. This work was cited by Linnaeus in 1758 for *Margaritifera margaritifera;* by Lightfoot[1] in 1786 for *Elliptio complanata;* and by Gmelin in 1791 for *Lampsilis radiata radiata*. It was not until January of 1817, when volume two of Nicholson's *First American Edition of the British Encyclopedia* appeared, which included Thomas Say's article on Conchology, that many of the common Atlantic Slope Unionidae were described and figured. Eleven of Say's species are recognized here. Many of these were redescribed two years later, in 1819, by Lamarck in volume VI of his *Histoire Naturelle des Animaux sans Vertèbres*. Only three of his names are recognized in this paper. In 1830 and 1831 Isaac Lea of Philadelphia describe several new species from the Southern Atlantic Slope region, and in 1834 Timothy A. Conrad published a little volume, *New Fresh Water Shells of the United States*, which included many of the species he had found in the southeastern states.

A bitter battle arose between Lea and Conrad over the priority of some of the species, but their polemics, discussed by Wheeler (1935), are only of historical interest. Lea continued to describe Unionidae from the Southern Atlantic Slope until 1874, by which time he had burdened the literature concerning the few species found there with over one hundred and fifty names. In this paper, nine of Conrad's taxa and fifteen of Lea's are considered valid.

With the demise of Isaac Lea, the describing of the Unionidae of the southeastern states, exclusive of Florida, was

[1] See p. 314.

essentially over. Between the years 1883–1934, the Wrights, father and son, described fifty-two species of mollusks, most of which were from Florida (Johnson, 1967a). The Wrights were a pair of unsophisticated naturalists who redescribed many species, and aside from *Villosa villosa*, which is described in this paper, their other relevant taxa are included in the various synonymies.

The Collectors

The first serious student of fresh-water mollusks to make a collecting trip to South Carolina and Georgia was Timothy A. Conrad. His route of 1833 is shown in detail by Wheeler (1935: 26, 27). Before and after this time, most collections were made by interested local residents who sent their material to Isaac Lea, and occasionally to Conrad, for description. In the 1830's Lea received Unionidae from Lewis Leconte, J. H. Couper, Professor Shepard, and Edmund Ravenel.

These men made it possible for Lea to describe most of the endemic species in the Altamaha River, Georgia. Later, Dr. J. P. Barratt sent him shells from the Abbeville District of South Carolina. From the Carolina's Lea received, in his later years, shells from E. Emmons and especially from C. M. Wheatley.

No extensive collecting took place on the Southern Atlantic Slope after Lea's time, until W. J. Clench and P. Okkelberg made a trip to Georgia in 1929. This trip was followed by another by Clench and H. van der Schalie in 1932; and then by Clench, C. V. MaCoy, and H. D. Russell in 1934. The collections made in 1929 and 1932 were shared by the Museum of Comparative Zoology and the University Museum, University of Michigan. The remaining collections are in the Museum of Comparative Zoology. In 1937 van der Schalie made a survey of the mollusks of the Ogeechee River, Georgia, for the Museum of Zoology, University of Michigan. The last major expedition to the Southern Atlantic Slope of Georgia was made by W. J. Clench, K. J. Boss, and S. L. H. Fuller in 1962, for the Museum of Comparative Zoology. Since then, Ruth Patrick (1967) of the Academy of Natural Sciences of Philadelphia has had J. Bates and S. L. H. Fuller make collections of Unionidae in the Savannah and other Atlantic Slope river systems, in connection with her limnological studies.

In 1950–51 W. M. Walter made an extensive survey of the Neuse River system, North Carolina. This collection was divided among the Museum of Comparative Zoology, United States National Museum, and Museum of Zoology, University of Michigan.

In the Carolinas and northward, collecting has been adequate, but not organized in a way that can be discussed. Many stations have been made by casual collectors, and Ortmann collected systematically in Virginia.

THE PRIMARY SYSTEMATIC STUDIES OF APALACHICOLAN AND ATLANTIC SLOPE UNIONACEA.

Charles T. Simpson's *Notes on the Unionidae of Florida and the Southeastern States* (1892) was the first attempt at a revision of any of the species of the Southern Atlantic Slope region. This work was followed (1900) by his *Synopsis of the Naiades*, which was expanded into the *Descriptive Catalogue of the Naiades* (1914). These two works include a revision of the Naiades on a worldwide basis. Simpson's species concepts, in so far as they concern the Apalachicolan and Atlantic Slope regions, have been generally accepted, with but few changes, until recently. His were scholarly works. Simpson was among the more competent malacologists of his time. He included in his works almost every taxon relevant to the North American Unionacea that had appeared before 1914.

After Simpson's work, aside from some

studies by Ortmann, little was done on the Unionacea of the Apalachicolan region until van der Schalie wrote the *Naiad Fauna of the Chipola River, in Northwestern Florida* (1940). This was followed by Clench and Turner's *Freshwater Mollusks of Alabama, Georgia, and Florida from the Escambia to the Suwannee River* (1956). Further additions were made by Athearn in *Three new unionids from Alabama and Florida and a note on Lampsilis jonesi* (1964) and by Johnson in *Additions to the unionid fauna of the Gulf drainage of Alabama, Georgia and Florida* (1967b).

The Unionacea of the Northern Atlantic Slope region were elegantly monographed by Ortmann, who wrote the *Naiades of Pennsylvania*, pt. 3 (1919). Recently, Clarke and Berg (1959) made a modern study of the *Freshwater Mussels of Central New York* which complemented Ortmann's work to the north. This work was followed by the *Freshwater Mussels of Nova Scotia* by Athearn and Clarke (1962).

This brief review of the primary literature on the Unionacea of the Apalachicolan and Atlantic Slope regions itself explains the reason for carrying the present study to the Potomac River. To have carried it further would have been redundant, in view of the quality of the work of Ortmann, Clarke and Berg, and Athearn and Clarke.

Classification of the Unionacea

The classification based on the anatomy of the genera of Unionacea proposed by Ortmann (1911, 1912a) is used here. Since Ortmann's time a few necessary nomenclatural changes have been made, but no one has substantially modified his concepts of the evolution of the North American genera.

In 1927 Frierson, an ardent naturalist and an oldfashioned typologist, published *A Classified and Annotated Check List of the North American Naiades*. He stated his method and philosophy:

> "Many generic divisions have been proposed, based upon characters of diverse kinds, some being those of the hard parts, others those of the soft parts. These characters resemble each other in the respect that they all vary very much, and that none are constant. The general plan adopted herein is to select groups which may be typed by one member, the rest being evident kinfolk. Such new genera as are named herein are unaccompanied by diagnoses, a type shell being named, whose chief characters will forever give such diagnoses."

The paper is sprinkled with numerous generic and subgeneric names. It is not unfair to say that most of these names would have fallen into obscurity except for two events. In 1934, Thiele, in his *Handbuch der Systematischen Weichtierkunde* (2, pt. 3: 815–844), fell under both the systematic and taxonomic influence of Frierson. This is understandable, as he was a compiler, not a specialist in the Unionacea, and Frierson's work was the latest synthesis, and should have been the last word.

In 1942, 1949, and 1964, Modell, in *Das natürliche System der Najaden*, proposed that the relationships within the Unionacea can be found in the beak sculpture. He proposed forty-three new names for family groupings. He expected his system to be accepted on the basis of a few diagrammatic sketches of beak sculpture, and faith in a single character, which I have not found constant. Regarding the North American Unionacea he says:

> " . . . after Simpson's divisions were not sufficient for these purposes [i.e. questions concerning nomenclature]. I had to go along completely with the uniform system of Frierson in order to give a better picture. With this however I also had to use Frierson's concepts of Rafinesque's names completely."[1]

Of course, as mentioned before, the objection is to Frierson's systematics. His nomenclatural eccentricities, in the sense implied by Modell, are not of concern here.

[1] Translation by Stansbery and Soehngen, 1964, Sterkiana, no. 14, p. 18.

In short, it is not implied that Ortmann's anatomical system is perfect, only that it has not been improved on. Haas (1969a), in *Superfamilia Unionacea*, does not use Modell's system of classification for the higher categories. His species concepts of the North American Unionacea are those of Frierson (1927), with a few additions. In *Superfamily Unionacea* Haas (1969b) only discusses the genera.

SYSTEMATIC SECTION

The following abbreviations have been used in the text and on the plate captions.

ANSP—Academy of Natural Sciences of Philadelphia, Pennsylvania

MCZ—Museum of Comparative Zoology, Cambridge, Massachusetts

MZUM—Museum of Zoology, University of Michigan, Ann Arbor, Michigan

USNM—United States National Museum, Washington, D. C.

Synonymy: For ease of reference, full citations are included for each taxon. Elsewhere in the text, references are abbreviated and require the use of the bibliography.

Isaac Lea often rushed brief Latin descriptions of his new species into print, a practice common in his time. These were subsequently followed by adequate descriptions and figures, which were then reprinted as "*Observations on the Genus Unio.*" Only page references to this work are included here since the plates and figures were never renumbered, but always kept the same numbers as in the preceeding reference. Lea generally gave several localities where each of his species had been found and did not select types, though he always figured a single specimen, for which he gave measurements. In lieu of the use of the word 'type,' under Article 73 (b) Int. Code Zool. Nomen. (1964), this is an "equivalent expression" and these specimens are regarded as holotypes. During the early part of the century, W. B. Marshall located most of these figured specimens in the United States National Museum. These have been rechecked, and their localities restricted when possible.

With but a few mentioned exceptions, all type localities were relocated, and are often rendered more specific from data on original labels and by references to standard atlases, modern county maps, or United States Geological Survey 1: 250,000 maps. These additional data are placed in square brackets.

Unless specifically mentioned to the contrary, all extant types have been examined and usually photographed. Almost none of Say's primary types have survived, and many of Conrad's are missing, whereas most of Lea's have been located.

Only pertinent references are included. Simpson (1914) is referred to only when our species concepts are similar or when the differences are easily reconcilable. The papers of Ortmann (1919), Clench and Turner (1956), Clarke and Berg (1959), and Athearn and Clarke (1962) are all referred to when relevant.

Descriptions: The measurements are only intended to convey the general size of specimens from a given station, or to illustrate sexual differences when they are relevant.

Anatomy and Breeding Season: These entries are included when such information is available. For widely distributed species, it should be borne in mind that the dates of the breeding season are not necessarily applicable to their entire range.

Habitat: Given when known:

Remarks: Statements made in this section, though applicable to each species over its entire range, are designed primarily to aid in differentiating one species from another within the Apalachicolan and Atlantic Slope regions.

Range: The ranges are intended to be all-inclusive for each species.

Records: The records, limited to the area of the study, are based mostly on speci-

mens in the major collections mentioned above under Abbreviations. All of these specimens have been examined, with a few noted exceptions. Sometimes similar records are found in several museums. If so, those in the Museum of Comparative Zoology are generally given preference. It is to be assumed that all records are in this museum, unless specifically mentioned to the contrary.

A few records from Virginia and Maryland, of common species, listed by Ortmann (1919) have not been reexamined, but are accepted with confidence. In each of these instances, references are given.

Walter (1956) did not list his data, but gave numbers on a figure of the Neuse River system. Because the first series of his collection is in the Museum of Comparative Zoology, his station numbers follow those of his localities which are included here. (See note on p. 323). The records of ubiquitous *Elliptio complanata* have been selected. They are more copious than is necessary to illustrate the distribution of the species, but they are an accurate index to the scope of collecting that has been done in the area covered in this portion of the paper.

In so far as possible, the records are arranged from headwaters to the mouth of the rivers, and from south to north, or west to east, as the case may be. Abbeville District, South Carolina, which occurs many times over in the records, includes the present counties of Abbeville and Greenwood, and most of McCormick.

Figures: When available, the holotypes are generally used to illustrate the various species. Often more than one illustration is included to show variability. Frequently, the data on the plate captions is not repeated elsewhere.

Key to the Unionidae Found Between the St. Marys River, Florida, and the Potomac River, Maryland.

The following key includes all of the species of Unionidae that are found between the St. Marys and the Potomac rivers, and it is designed to be used with specimens primarily from this area. The key in Clarke and Berg (1959: 13) may be used for the identification of the northeastern species of Unionacea. The key is artificial and is based on shell characters only. Some species of Unionidae are quite variable and some specimens may not key out correctly. Therefore it is advisable to confirm identifications made with the key by reference to the text and figures.

1. Hinge teeth completely absent. 4
   Articulating or vestigial hinge teeth present. 2
2. Hinge teeth vestigial. 3
   Articulating pseudocardinal teeth present. 8
3. Radial wrinkles on the posterior slope, each valve with one thin, depressed triangular pseudocardinal tooth; no lateral teeth ..... *Alasmidonta varicosa* p. 354
   Radial wrinkles absent on the posterior slope, each valve with a slight depression and then a slightly raised thickening just before the umbos ..... *Strophitus undulatus* p. 367
4. Umbos inflated, raised above the hinge line. 5
   Umbos flat, not raised above the hinge line. 7
5. Shell greatly inflated, especially toward the posterior ventral margin; Altamaha River system only ..... *Anodonta gibbosa* p. 359
   Shell somewhat inflated, but uniformly so. 6
6. Shell uniformly thin, nacre bluish white ..... *Anodonta cataracta cataracta* p. 356
   Shell prominently thickened along the anterior ventral margin below the pallial line; nacre salmon or copper colored ..... *Anodonta implicata* p. 360
7. Dorsal and ventral margins almost parallel; periostracum with broad green rays. Shell very thin and not much inflated ..... *Anodonta imbecilis* p. 362
   Ventral margin very broadly curved; periostracum with fine green rays. Shell very thin and not much inflated ..... *Anodonta couperiana* p. 365
8. Lateral teeth absent or vestigial. 9
   Articulating lateral teeth present. 11
9. Posterior ridge very rounded; shell elliptical or subrhomboid ..... *Alasmidonta undulata* p. 349
   Posterior ridge sharp; shell subtriangular. 10
10. Umbos anterior to the center, incurved; posterior slope acute ..... *Alasmidonta triangulata* p. 351
    Umbos centrally located, acutely incurved; posterior slope at almost 90° angle with

posterior ridge; Altamaha River system only ..... *Alasmidonta arcula* p. 352

11. Lateral teeth double in the right valve, single in the left one. Shell quite small ..... *Alasmidonta heterodon* p. 347
Lateral teeth single in the right valve, double in the left one. 12
12. Pseudocardinal teeth chunky and serrated, the more prominent one in the right valve not parallel to the hinge line. 13
Pseudocardinal teeth long and lamellate, with a tendency of the larger one in the right valve to be parallel to the hinge line. 29
13. Shell less than, or about, twice as long as high. 14
Shell distinctly more than twice as long as high. 37
14. Posterior ridge with faint ridges crossing lines of growth. 15
Posterior ridge without faint ridges crossing line of growth. 20
15. Shell subrhomboidal, subtriangular or quadrate, often solid, sometimes quite ponderous. 16
Shell subelliptical or elongated rhomboid, generally quite thin. 19
16. Posterior ridge of variable acuteness. 17
Posterior ridge sharp; shell rather thin, with green rays; Altamaha River system only ..... *Elliptio dariensis* p. 310
17. Shell ponderous, not rayed, or with thin dark green rays when young, generally blackish; St. Marys River system only ..... *Elliptio c. crassidens* p. 305
Shell not ponderous, with green rays of varying width, yellowish or chestnut ..... *Elliptio congaraea* p. 308
18. Posterior ridge sharp near the umbos, becoming faint and biangulate toward the posterior margin. Shell compressed, brownish. Young specimens occasionally with faint green rays ..... *Elliptio fraterna* p. 312
Posterior ridge consistently acute. Shell subinflated, brownish, often with narrow green rays over entire surface ..... *Elliptio waccamawensis* p. 313
19. Shell ponderous, inflated; posterior ridge double and of variable acuteness, brownish, rhomboid to obovate; Satilla River system only ..... *Elliptio c. downiei* p. 307
Shell not ponderous, disks flattened; posterior ridge double, but uniformly rounded. 20
20. Dorsal margin long, forming an acute angle with the obliquely descending posterior margin. 21
Dorsal margin very long, forming an extremely acute angle with the obliquely descending posterior margin, rendering the posterior end rather wedge shaped. 22
21. Shell rather uniformly trapezoidal, disk flattened; periostracum not usually shiny, often rayed, yellowish green to black ..... *Elliptio complanata* p. 314
Shell subrhomboidal, often somewhat pointed, very variable as to shape and degree of inflation; periostracum usually subshiny to shiny, often rayed, yellowish to brownish ..... *Elliptio icterina* p. 325
22. Valves with greatest degree of inflation at midpoint of posterior ridge; shell often rayed when young, becoming blackish with age. Periostracum smooth on the disk, rough toward the margins; Altamaha River system only *Elliptio hopetonensis* p. 324
Valves rather uniformly inflated; shell not rayed, occasionally greenish when young, becoming blackish with age. Periostracum generally distinctly satiny ..... *Uniomerus tetralasmus* p. 339
23. Shell small, not exceeding 65 mm in length, seldom rayed; periostracum yellowish, greenish, or brownish. Sexual dimorphism generally present. 24
Shell large, generally rayed, periostracum greenish yellow. Sexual dimorphism present. 28
24. Shell without spines on disk. 25
Shell with spines on disk. Outline subquadrate or subrhomboid; periostracum yellowish or brownish. Sexual differences not well marked ..... *Pleurobema collina* p. 300
25. Shell with a constriction of the ventral margin before a double, but faint, posterior ridge; periostracum smooth. 26
Shell with a regularly rounded ventral margin before a sharp double posterior ridge; periostracum with numerous heavy ridges. Outline of female long obovate; outline of male elliptical ..... *Carunculina pulla* p. 370
26. Outline subquadrate or rhomboid; periostracum often clothlike, blackish brown, occasionally with rays. Sexual difference not well marked ..... *Pleurobema masoni* p. 301
Outline of female short obovate; of male subelliptical. Periostracum yellowish green, with fine green rays over the entire surface ..... *Villosa constricta* p. 378
27. Outline a long ellipse; greenish rays over entire surface, periostracum satiny and clothlike ..... *Villosa villosa* p. 372
Shell not as above and much larger. 28
28. Posterior ridge well developed, especially toward the umbos. Shell subovate with narrow or wide rays generally distributed over a rather shiny yellowish background.

Sexual differences well marked in the shell ..... *Lampsilis ovata* p. 386
Posterior ridge low and rounded. Shell subelliptical, with wide rays generally distributed over a dull yellowish green background. Sexual differences not always well marked in the shell ..... *Lampsilis radiata radiata* p. 390

29. Left valve without a rudimentary interdental projection. 30
Left valve with a rudimentary projection, which fits into an interdental groove in the right valve; shell generally small, 45 to 65 mm in length, though giant specimens occur; subrhomboid, often with a low posterior wing when young ..... *Lasmigona subviridis* p. 343

30. Shell without spines on surface. 31
Shell with hollow spines in front of a sharp posterior ridge. Outline subtriangular; nacre purple. Altamaha River system only ..... *Elliptio spinosa* p. 303

31. Posterior ridge present and well defined, at least toward the umbos. Shell rather large and solid, yellowish, with varying amounts of the surface covered with green rays. Sexual dimorphism present. 32
Posterior ridge very broadly rounded. Shell small and thin, with numerous green rays over the entire surface, more greenish than yellow. 35

32. Surface of the shell either without rays or with some on posterior slope only. Periostracum shiny. 33
Surface of the shell with rays over the entire surface. Periostracum more often subshiny than shiny. 34

33. Posterior ridge low and rounded except toward the umbos, interdentum present. Nacre bluish white ..... *Lampsilis cariosa* p. 382
Posterior ridge very sharp, interdentum present; Altamaha River system only ..... *Lampsilis dolabraeformis* p. 384

34. Nacre bluish; rays narrow. Posterior ridge rounded except toward the umbos. Shell thin, no interdentum ..... *Lampsilis ochracea* p. 388

35. Periostracum shiny. 36
Periostracum distinctly satiny. ..... *Villosa villosa* p. 372

36. Narrow green rays, interrupted by growth rests ..... *Villosa delumbis* p. 375
Wide green rays, not interrupted by growth rests ..... *Villosa vibex* p. 373

37. Shell with ventral margin incurved, often sufficiently as to render entire shell arcuate. 38
Shell with ventral margin straight or curved, sometimes with a slight dorsal-ventral sulcus. Dorsal and ventral margins roughly parallel. 39

38. Shell somewhat over twice as long as high, subelliptical, posterior end produced; seldom rayed ..... *Elliptio arctata* p. 331
Shell over three times as long as high, trapezoidal, with the highest point at the anterior end tapering to a long point; rays visible when young. Altamaha River only ..... *Elliptio shepardiana* p. 338

39. Nacre silvery white; posterior end distinctly lance-head shaped; rays always present. Sexual dimorphism present. Females with a distinct postbasal swelling. ..... *Ligumia nasuta* p. 380
Nacre coppery or purple; dorsal and ventral margin almost parallel, often rayed, somewhat over twice as long as high ..... *Elliptio lanceolata* p. 333

Superfamily **Unionacea** Thiele 1935[1]

Family **Unionidae** (Fleming 1828) Ortmann 1911

Subfamily **Unioninae** (Swainson 1840) Ortmann 1910

Genus *Pleurobema* Rafinesque

Subgenus *Pleurobema s.s. Rafinesque*

Pleurobema Rafinesque 1819, Jour. Phys. Chim. Hist. Nat. (Paris), 88: 427. Species listed: *P. mytiloides* Rafinesque, *P. conica* ? Rafinesque [*nomina nuda*]. Rafinesque, 1820, Ann. Gén. des Sci. Phys. (Bruxelles), 5: 313. Species listed: *P. mytiloides* Rafinesque, *P. cuneata* Rafinesque.

Type species, *Unio mytiloides* Rafinesque. Subsequent designation, Herrmannsen, 1847, Indicis Generum Malacozoorum, 1: 292.
Ortmann, 1912, Ann. Carnegie Mus., 8: 261. Ortmann and Walker (1922, Occ. Pap. Mus. Zool., Univ. Mich. no. 112, p. 20) state that the description of *P. mytiloides* in 1820 rendered the genus monotypic. This is not so, as the first use of *P. mytiloides* has no bearing on the subsequent recognition of the genus.

Under *Pleurobema s. s.*, Frierson (1927: 40–44) includes thirty-seven species and subspecies. It is probable that some of these taxa will be subsequently reduced to synonymy, but it is clear that this genus

[1] Or, Unionoidea (*oidea* is the standard ending for superfamily names, though *acea* has been generally used in molluscan taxonomy).

has achieved its greatest diversity in the Interior Basin.

Subgenus *Lexingtonia* Ortmann

Lexingtonia Ortmann 1914, Nautilus, 28: 28.
Type species, *Unio subplanus* Conrad. Original designation.

Ortmann instituted *Lexingtonia* as a genus because he believed that the six to eight subconcentric ridges of the beak sculpture and the red placentae differentiated it from *Elliptio* and *Pleurobema*. He mentions that the shell resembles *Fusconaia* in which all four gills serve as marsupia, but since he also says that only the outer gills are so used by *U. subplanus* Conrad = *masoni* Conrad, as in *Pleurobema,* the present author is placing *Lexingtonia* under *Pleurobema* as a subgenus, as did Frierson (1927: 44).

Under *Lexingtonia*, Frierson (1927: 44, 45) includes three species. Two of these are included here under the synonymy of *Pleurobema* (*Lexingtonia*) *masoni* (Conrad). The third, *Pleurobema utriculum* (Lea) belongs to the Tennessee River drainage. Its synonymy has not been reinvestigated, but it probably does not belong in this subgenus, which appears to be restricted to the Southern Atlantic Slope.

Pleurobema (*Lexingtonia*) *collina* (Conrad) Plate 2: 1–2

Unio collinus Conrad 1836, Monography Unionidae, no. 7, pl. 36, fig. 2 [plate caption only]. 1837, *op. cit.*, no. 8, p. 65 (North [= Maury] River, a branch of the James River [Rockbridge Co.], Virginia; type lot ANSP 20408 [lost]). 1840, *op. cit.*, no. 12, p. 109, pl. 60, fig. 3; this subsequently figured metatype, here selected, lectotype ANSP 41007.
Alasmidonta collina (Conrad). Simpson, 1914, Cat. Naiades, 1: 501.
Pleurobema collina (Conrad). Boss and Clench, 1967, Occ. Papers on Moll., 3: 45–51.

Description. Shell small, seldom reaching more than 55 mm in length. Outline subquadrate or subrhomboid. Valves subcompressed, subsolid. Anterior end regularly rounded; posterior end angular and slightly cut away below. Ventral margin straight or slightly arcuate centrally. Dorsal margin almost straight, terminating in a sharp angle with the obliquely truncated posterior margin. Hinge ligament short but prominent. Posterior ridge full, rounded, weakly biangulate toward the base of the shell. Umbos slightly elevated and located somewhat anterior to the middle of the shell, their sculpture consisting of three to four strong subconcentric ridges that form an indistinct rounded angle on the posterior ridge. Surface of the disk smooth, with undifferentiated concentric growth rings, surface sculptured with short differentiated bilateral spines especially in the region of the posterior dorsal slope and posterior quarter of the disk. Periostracum bright yellow or greenish yellow in young shells, becoming brownish in adults; rarely rayed with fine, narrow, broken, brownish lines.

Left valve with two ragged, triangular pseudocardinal teeth and two short, obliquely descending parallel lateral teeth. Right valve with one ragged, triangular pseudocardinal with a vestigial tooth above it; one lateral tooth. Beak cavities compressed; anterior adductor muscle scars deep, posterior ones very faint. Pallial line distinct, especially anteriorly. Nacre white, occasionally slightly pinkish, often bluish posteriorly.

Length mm	Height mm	Width mm	
55.0	34.7	20.3	Rivanna River, 2 mi. W Columbia, Fluvanna Co., Virginia.
46.0	30.0	19.0	North River [Rockbridge Co.], Virginia. Lectotype.

Anatomy. Discussed by Boss and Clench (1967: 47).

Breeding season. Probably tachytictic, releasing the glochidia during the summer. (Boss and Clench, 1967: 48.)

Habitat. Lives on sandy bottoms, in rather swift water.

Remarks. Pleurobema collina (Conrad) is a distinct Southern Atlantic Slope species. It is remarkable for the spines on the posterior slope of the valves. Usually the maximum number of pairs is three, and, in general, they are nearly bilaterally symmetrical. The first set of spines is about 3–4 mm from the umbo, the second 6–8 mm, and the third from 10–17 mm. The largest spines approach 5 mm in length and have a thickness of more than 1.5 mm. The spines are originally hollow, being closed ventrally at the end of their formation. (Boss and Clench, 1967: 47.)

Boss and Clench (1967) convincingly pointed out the similarity of *P. masoni* and *collina*. When the latter does not have spines, the two species can be easily confused, except that *masoni* is slightly more rhomboid and often has a brownish cloth-like periostracum, generally with at least a trace of green rays on the disk, whereas *collina* has a periostracum that is more yellowish and smooth, with only an occasional hint of brownish rays.

The range of this species was extended by Miss Carol Stein, who collected two small specimens in the Tar River in 1964.

Range. Southern Atlantic Slope: Tar River, of the Pamlico River system, North Carolina, and James River system, Virginia.

Specimens Examined

Pamlico River System

Tar River Drainage. *North Carolina*: Tar River, Old Sparta, 3.5 mi. W Pine Tops, Edgecombe Co. (Ohio State Museum).

James River System

James River Drainage. *Virginia*: Calfpasture River (Conrad, 1846: 407); North [= Maury] River, Lexington; James River, near Natural Bridge (USNM), *all* Rockbridge Co. James River, Buchanan, Botetourt Co. Rivanna River, 2 mi. W Columbia, Fluvanna Co. James River, opposite Maidens, Goochland Co.

Pleurobema (*Lexingtonia*) *masoni* (Conrad)

Plate 2: 3–10

Unio masoni Conrad 1834, New Fresh Water Shells United States, p. 34, pl. 5, fig. 2 (Savannah River, Augusta [Richmond Co.], Georgia; figured holotype ANSP 41333). Conrad, 1836, Monography Unionidae, no. 3, p. 28, pl. 12, fig. 2; figured paratype ANSP 41332.

Unio subplanus Conrad 1837, Monography Unionidae, no. 9, p. 73, pl. 41, fig. 1 ([North = Maury River, a] branch of the James River, Lexington, Rockbridge Co., Virginia; holotype ANSP 20412 [lost]).

Unio pumilus Lea 1838, Trans. Amer. Philos. Soc., 6: 23, pl. 7, fig. 17 (Black River [a tributary of the Neuse River] on the road to Fayetteville from Smithfield [= about 10 mi. W of Benson, Johnston Co.], North Carolina; figured holotype USNM 84545). Lea, 1838, Obs. Unio, 2: 23.

Unio merus Lea 1852, Trans. Amer. Philos. Soc., 10: 260, pl. 15, fig. 10 (Abbeville District [Savannah River drainage], South Carolina; figured holotype USNM 85698). Lea, 1852, Obs. Unio, 5: 16.

Unio striatulus Lea 1857, Proc. Acad. Nat. Sci. Phila., 9: 86 (Roanoke River, Weldon [Halifax Co.], North Carolina). Lea, 1862, Jour. Acad. Nat. Sci. Phila., ser. 2, 5: 55, pl. 2, fig. 202; figured holotype USNM 84548. Lea, 1862, Obs. Unio, 8: 59.

Unio castus Lea 1860, Proc. Acad. Nat. Sci. Phila., 12: 306 (South Carolina). Lea, 1860, Jour. Acad. Nat. Sci. Phila., ser. 2, 4: 349, pl. 57, fig. 174; figured holotype USNM 84782. Lea, 1860, Obs. Unio, 8: 31.

Unio brimleyi S. H. Wright 1897, Nautilus, 10: 138 ([Walnut Creek of] Neuse River, Raleigh [Wake Co.], North Carolina; lectotype USNM 149651, selected by Johnson, 1967, Occ. Papers on Moll., 3: 5, pl. 5, fig. 1. The type locality was restricted to Walnut Creek on the basis of Brimley's previously unpublished notes (Walter, 1956: 268).

Lexingtonia subplana (Conrad). Ortmann, 1914, Nautilus, 28: 29.

Description. Shell small, seldom reaching more than 50 mm in length. Outline subquadrate or rhomboid. Valves subcompressed, subsolid. Anterior end regularly rounded; posterior end angular and slightly cut away below. Ventral margin straight save for a slight undulation posteriorly. Dorsal margin straight, terminating in a sharp angle with the obliquely truncated posterior margin. Hinge ligament

short but prominent. Posterior ridge full, rounded, often with a second or tertiary ridge ending in slight biangulations toward the base of the shell. Umbos slightly elevated, located somewhat anterior to the middle of the shell, their sculpture consisting of six to eight rather crowded subconcentric ridges that form an indistinct rounded angle on the posterior ridge, in front of which they are wavy and corrugated. Disk often with irregular incremental striae, which sometimes render the periostracum rather clothlike; greenish, yellowish, or yellowish brown, sometimes with dark, dull greenish rays.

Left valve with two ragged, triangular pseudocardial teeth and two short, oblique descending, parallel lateral teeth. Right valve with one ragged, triangular pseudocardial with a vestigial tooth above it; one lateral tooth, which is sometimes double. Beak cavities compressed; anterior adductor muscle scars deep, posterior ones very faint. Pallial line distinct anteriorly only. Nacre white or bluish white, thinner and somewhat irridescent posteriorly.

Length mm	Height mm	Width mm	
62	41	22	Nottoway River, 3 mi. E Rawlings, Brunswick Co., Virginia.
47	28	19	Mill Race, 2 mi. N Sardis, Burke Co., Georgia.
31	21	14	Ogeechee River, Shoals, 12 mi. S Warrington, Warren Co., Georgia.

Anatomy. Discussed by Ortmann, 1914, Nautilus, 28: 29–30. "Glochidia semi-elliptical, without hooks. Length and height the same, 0.18 mm."

Breeding season. Ortmann found a gravid female in the North River, Lexington, Rockbridge Co., Virginia, on June 7, 1912.

Habitat. Lives on sandy bottoms, in rather swift water.

Remarks. Pleurobema masoni (Conrad) is a distinct Atlantic Slope species. It is closest to *P. pyriforme* (Lea) (figured by Clench and Turner, 1956: 162, pl. 8, fig. 6) which ranges from the Apalachicola to the Suwannee River system. The latter species is decidedly more subovate, with the posterior end tending to be broadly pointed. The ventral margin is rarely arcuate posteriorly; the disk is less compressed. The periostracum is often blackish or yellowish brown, but seldom rayed.

Except for examples of *P. masoni* from the Nottoway and James rivers, near the northern limit of its range, where the shells reach their maximum size and are found in relative abundance, this is a very rare species. In most drainage systems it is known from but a few examples. In 1961, Clench, Boss, and Fuller collected several thousand Unionidae in Georgia, but found only seven specimens of this species from two localities.

In the James River, Virginia, *P. masoni* is found closely associated with *P. collina*, under which see: *Remarks* on p. 301.

Range. Southern Atlantic Slope: Ogeechee River system, Georgia, north to the James River system, Virginia.

Specimens Examined

Ogeechee River System

Ogeechee River Drainage. *Georgia*: Ogeechee River, 12 mi. SW Warrington, Warren Co. Buckhead Creek, 10 mi. SW Sardis, Burke Co.

Savannah River System

Savannah River Drainage. *South Carolina:* Abbeville District (USNM). *Georgia:* Broad River [Madison or Elbert Co.] (MZUM). Savannah River, Augusta, Richmond Co. (ANSP). Mill Race, 2 mi. N Sardis, Burke Co.

Cooper-Santee River System

Catawba River Drainage. *North Carolina:* Long Creek, Gaston Co.

Pedee River System

Yadkin River Drainage. *North Carolina:* Salem, Forsyth Co. (MZUM).

Cape Fear River System

Cape Fear River (MZUM).

Neuse River System

Neuse River Drainage. *North Carolina*: Hillsboro, Orange Co. Eno River, 6 mi. NNW Durham Center, Durham Co. (112). Walnut Creek, Raleigh (USNM); Neuse River, Raleigh; Little River, 2 mi. WSW Zebulon (6); *all* Wake Co. Black Creek [about 10 mi. W Benson, Johnston Co.] (USNM).

Pamlico River System

Tar River Drainage. *North Carolina*: Tar River, Providence, Granville Co. Tar River, Bruce, 9 mi. NW Greenville; Chicod Creek, 8 mi. W Greenville; *both* Pitt Co.

Roanoke River System

Roanoke River Drainage. *North Carolina*: Roanoke River, Weldon, Halifax Co.

Chowan River System

Nottoway River Drainage. *Virginia*: Nottoway River, 3 mi. E Rawlings, Brunswick Co.

James River System

James River Drainage. *Virginia*: Calfpasture River (Conrad, 1846: 407); North [=Maury] River, Lexington (ANSP); North River, above Buena Vista (Carnegie Mus.); [North River] Natural Bridge; *all* Rockbridge Co. Rivanna River, 2 mi. W Columbia, Fluvanna Co. James River, opposite Maidens, Goochland Co. James River, Richmond, Henrico Co. (MZUM).

Genus *Elliptio* Rafinesque

Subgenus *Canthyria* Swainson

Canthyria Swainson 1840, Treatise on Malacology, pp. 276, 378.

Type species, *Unio spinosus* Lea. Original designation.

Ortmann (1912, Ann. Carnegie Mus., 8: 269) suggests that "the spines [of the type] are unique, and would possibly justify the erection of a separate genus: *Canthyria*" for this species. Simpson (1914, 2: 704) states that the anatomy of *spinosa* is typical of *Unio* [=*Elliptio*]. Frierson (1927: 50) used this name as a genus to include both *spinosa* and *Pleurobema collina* (Conrad) on the basis of the spines. Boss and Clench (1967: 50) have clearly shown that these two species are of different lineages, and that the spines are a convergent character. In spite of the anatomical similarity to *Elliptio*, the shell morphology is not close to that of any other member of the genus. This appears to be a very old species, which is restricted to the Altamaha River system, Georgia.

This subgenus is monotypic.

Elliptio (*Canthyria*) *spinosa* (Lea)

Plate 2: 11

Unio spinosus Lea 1836, Description of a new *Unio*, pp. 1–4 (col. figs.) [not seen]. Lea, 1838, Trans. Amer. Philos. Soc., 6: 57, pl. 16, fig. 50 (Altamaha [River], Hopeton, near Darien [McIntosh Co.], Georgia; figured type in collection of Prof. Shepard [presumed lost]; Altamaha [River], Liberty [now Long] Co., Georgia). Lea, 1838, Obs. Unio, 2: 57. Simpson, 1914, Cat. Naiades, 2: 702.

Description. Shell medium to large, reaching 110 mm in length. Outline subrhomboidal or subtriangular. Valves subinflated to inflated, inequilateral, or almost equilateral; shell solid. Anterior end regularly rounded; posterior end slightly broader, ending in a point just below the medial line. Ventral margin slightly curved. Dorsal margin obliquely descending from the umbos, imperceptibly joining the descending posterior margin. Hinge ligament prominent, but short. Posterior ridge sharply angular, often with a faint secondary ridge above it, which renders the posterior slope slightly rugose. Umbos slightly elevated above the hinge line, located in the anterior third of the shell, their sculpture consisting of several very tiny bars. Surface of the shell generally smooth and shiny with fine concentric sculpture.

Each valve ornamented with from one to five spines of various length (varying from 1–2.5 mm in length) straight or crooked, usually arranged in a row, roughly parallel to the posterior ridge. Periostracum greenish yellow or brownish in old shells, usually with faint greenish and yellowish rays.

Left valve with two pseudocardinal teeth, one in front of the other, the anterior one somewhat triangular, the hinder one vestigial. Hinge line short and narrow, two obliquely descending straight lateral teeth. Right valve with two roughly parallel pseudocardinals, the posterior one triangular and serrated, the more anterior one low and vestigial; one lateral tooth. Beak cavities moderately deep, with a few dorsal muscle scars. Anterior and posterior adductor muscle scars well impressed. Pallial line distinct. Nacre pinkish or purplish, seldom white.

The spine is a tubular growth which appears to contain a lobe of the mantle until it has reached its full height, at which time the lobe fills the hollow spine with shell as it retreats.

Length mm	Height mm	Width mm	
110	54	48	Oconee River, 2.5 mi. N Glenwood, Montgomery Co., Georgia.
89	54	37	As above.
69	43	35	Altamaha River, 4 mi. NE Jesup, Wayne Co., Georgia.

Anatomy. Discussed by Lea (1863: 413). The anatomy is typical of *Unio* [=*Elliptio*] according to Simpson (1914, 2: 704).

Habitat. Lives buried from two to four inches deep in sand bars, in swift water.

Remarks. Elliptio spinosa (Lea) is known only from the Altamaha River system of Georgia. It is remarkable for the long spines that run parallel to the posterior ridge that are erected near growth rests during the first few years. None of the some sixty specimens seen have spines that are started after the shells had reached a height of about 30 mm. Presumably it is while the animal is young that the spines are most useful as grappling devices for holding the shells in sand.

Pleurobema collina (Conrad) of the Tar and James rivers of North Carolina and Virginia is also spined. This led Frierson (1927: 46) to unite the two species under the genus *Canthyria* Swainson 1840, but Boss and Clench (1967: 50) have clearly shown that the two species are of different lineages, and that the spines are a convergent character.

The distinct triangular shape; the equally distinctive greenish yellow, finely rayed, periostracum; the pink or purplish nacre; and the long spines distinguish *E. spinosa* from all other Atlantic Slope unionids.

In his "Travels of William Bartram," the well-known botanist mentions seeing this shell in 1773, probably near Frederica [Glynn Co., Georgia], but writing his journal from memory some thirteen years later, he claims to have seen it in the Mississippi River, Louisiana (Goodrich, 1930: 140).

Range. Southern Atlantic Slope: restricted to the Altamaha River system, Georgia.

Specimens Examined

Altamaha River System

Ocmulgee River Drainage. *Georgia*: Ocmulgee River, below Lumber City, Telfair Co. (H. D. Athearn).

Oconee River Drainage. *Georgia*: Oconee River, 2.5 mi. N Glenwood, Montgomery Co.

Altamaha River Drainage. *Georgia*: Altamaha River, 10 mi. ENE Surrency, Appling Co. Altamaha River, 11 mi. N Odum; Altamaha River, 4 mi. NE Jesup; *both* Wayne Co. Altamaha River, Fort Barrington; Altamaha River, Hopeton, near Darien; *both* McIntosh Co.

Subgenus *Elliptio s.s.* Rafinesque

Elliptio Rafinesque 1819, Jour. Phys. Chim. Hist. Nat. (Paris), 88: 426 [*nomen nudum*]. Rafi-

nesque, 1820, Ann. Gén. Sci. Phys. (Bruxelles), 5: 291. Species listed: *E. nigra* Rafinesque, *E. crassa* (Say), *E. viridis* Rafinesque, *E. fasciata* Rafinesque.

Type species, *Unio nigra* Rafinesque. Subsequent designation, Ortmann, 1912, Ann. Carnegie Mus., 8: 266. The previous use of *Unio crassidens* Lamarck as type species by Simpson (1900, Proc. U. S. Natl. Mus., 22: 700) is invalid since Lamarck's name was not included by Rafinesque in his list of species.

Eurynia Rafinesque 1819, Jour. Phys. Chim. Hist. Nat. (Paris), 88: 426 [*nomen nudum*]. Rafinesque, 1820, Ann. Gén. Sci. Phys. (Bruxelles), 5: 297. Species listed: *Unio dilatata. Unio latissima, Unio solenoides, all* Rafinesque.

Type species, *Unio dilatatus* [sic] Rafinesque. Subsequent designation, Herrmannsen, 1847, Indicis Generum Malacozoorum, 1: 436.

Cunicula Swainson 1840, Treatise on Malacology, pp. 268, 378. Species listed: *C. planulata* Lea, *C. patula* Lea, *C. rubiginosa* Lea, *C. secura* Lea, *C. purpurascens* Lamarck.

Type species, *Unio purpurascens* Lamarck. Subsequent designation, Herrmannsen, 1847, Indicis Generum Malacozoorum, 1: 335. Ortmann and Walker (1922, Occ. Pap. Mus. Zool., Univ. Mich. no. 112, p. 28) selected *Elliptio* over *Eurynia* on the basis of page precedence.

Although *Elliptio* has been usually treated as a masculine noun, H. B. Baker (1964, Nautilus, 78: 33) has pointed out that Rafinesque consistently used *Elliptio* as feminine (e.g. *E. nigra*) and therefore the name should be thus treated.

Elliptio s. s. is represented by *Elliptio crassidens* (Lamarck) and *E. dilatata* (Rafinesque), (figured by: Ortmann, 1919: 95, pl. 8, fig. 2) in the Interior Basin, where they are widespread and locally abundant. At present, it is a moot question whether the several subgenera from Central America, included by Frierson (1927: 33–39) under *Elliptio,* belong there, but if they do, the evidence is that the area comprised of Mexico and Central America is one where considerable speciation has occurred in this genus.

Speciation within *Elliptio s. s.* has occurred primarily in the Apalachicolan region, Peninsular Florida, and the Southern Atlantic Slope region. In these regions the species of *Elliptio s. s.* are the most abundant Unionidae. *Elliptios* are often found in environments in which no other genera of Unionidae live, since some of them have an unusually wide environmental tolerance, even to silting and pollution. As a consequence, some of the species have developed many ecophenotypes, and at a given station there often appears to be less interspecific variation than infraspecific variation between localities. This variation has led to a plethora of names being applied to the several species.

Elliptio (Elliptio) crassidens crassidens (Lamarck)

Plate 3: 1–3

Unio crassidens var. b Lamarck 1819, Hist. Nat. des Animaux sans Vertèbres, 6: 71 (lac Erie [erroneous]; lectotype, Paris Museum, selected by Johnson, 1969, Nautilus, 83: 53, fig. 2, and the type locality restricted to the Ohio River, Cincinnati, Ohio). A composite species, restricted by Lea (1834, Proc. Amer. Philos. Soc., 5: 87), as first revisor, on the basis of his identification of the type = *Unio cuneatus* Barnes. See: Ortmann and Walker (1922: 28).

Unio nigra Rafinesque 1920, Ann. Gén. Sci. Phys. (Bruxelles), 5: 291, pl. 80, figs. 1–4 (Ohio River; type ANSP 20243, *teste*, Vannetta, 1915, Proc. Acad. Nat. Sci. Phila., 66: 555).

Unio cuneatus Barnes 1823, Amer. Jour. Sci., 6: 263 (Ohio River; type [lost]).

Unio incrassatus Lea 1840, Proc. Amer. Philos. Soc., 1: 268 (Chattahoochee River, near Columbus [Muscogee Co.], Georgia). Lea, 1840, Trans. Amer. Philos. Soc., 8: 217, pl. 16, fig. 34; figured holotype USNM 84537). Lea, 1842, Obs. Unio, 3: 55.

Unio discus Sowerby 1868, *in* Reeve, Conch. Iconica 16, *Unio*, pl. 62, fig. 310 (India) *non* Lea 1838.

Unio lehmanii S. H. Wright 1897, Nautilus, 10: 138 (St. Marys River, [Nassau Co.], Florida; lectotype USNM 149650 selected by Johnson, 1967, Occ. Pap. Moll., 3: 7, pl. 6, fig. 3).

Unio danielsii B. H. Wright 1899, Nautilus, 13: 31 (Spring Creek [a branch of the Flint River], Decatur Co., Georgia; measured holotype USNM 168967, figured by Johnson, 1967, Occ. Pap. Moll., 3: 5, pl. 6, fig. 1).

Unio polymorphus B. H. Wright 1899, Nautilus, 13: 42 (Spanish Creek [a tributary of the St. Marys River, W of Folkston], Charleton Co., Georgia; lectotype USNM 152060 selected by

Johnson, 1967, Occ. Pap. Moll., 3: 8, pl. 6, fig. 2).

Elliptio pachyodon Pilsbry 1953, Pliocene Moll. Southern Florida, Acad. Nat. Sci. Phila., Monog. 8, p. 447, pl. 65, fig. 8 (St. Petersburg [Hillsboro Co.], Florida; type ANSP 18586; Pliocene).

Elliptio niger Rafinesque. Ortmann 1919, Mem. Carnegie Mus., 8: 91, pl. 8, fig. 1.

Elliptio crassidens incrassatus (Lea). Clench and Turner, 1956, Bull. Florida State Mus., 1: 171, pl. 8, fig. 1.

Description. Shell often large, exceeding 130 mm in length, though usually not exceeding 100 mm in the Atlantic drainage. Outline subrhomboid, or quadrate, somewhat produced posteriorly in older specimens. Valves somewhat inflated, rather solid to ponderous, inequilateral. Anterior end regularly rounded; posterior end more broadly rounded and either somewhat pointed or biangulate. Ventral margin straight or slightly curved, sometimes arcuate in matures. Dorsal margin broadly rounded, usually indistinctly joining the obliquely descending posterior margin. Hinge ligament prominent, located posteriorly. Posterior ridge generally sharp and angular, especially when young, often becoming more broadly rounded with age. Posterior ridge generally double. Secondary ridge varying greatly as to prominence and distance from the primary ridge. This variation causes a considerable range as to degree of terminal biangulation, and further causes the posterior slope to vary from subtruncated to broad. Posterior slope generally with a few wrinkles radiating from posterior ridge to dorsal margin. Umbos rather full, but rather low, located in anterior third of shell, their sculpture consisting of a few coarse ridges running parallel to growth lines. Young shells may be rather smooth on the disk, developing concentric striae with age; posterior slope usually becoming more wrinkled. Periostracum fine when young, reddish brown or chestnut, sometimes yellowish with greenish rays; posterior slope generally darker. In older specimens, periostracum generally uniformly black. Left valve with two heavy, rough pseudocardinal teeth, the more anterior one smaller and lower. Hinge line rather short and broad, with two short, slightly curved lateral teeth. Right valve with one chunky serrated pseudocardinal; one lateral tooth. Beak cavities very shallow, with a few dorsal muscle scars under the hinge plate. Anterior adductor muscle scars very deep, posterior ones and pallial line distinct. Nacre usually purplish, salmon, sometimes yellowish, posteriorly iridescent.

Length mm	Height mm	Width mm	
94	57	38	Spanish Creek, Charleton Co., Georgia.
71	40	28	As above.
62	40	30	As above.
54	36	23	As above.

Anatomy. Discussed by Lea (1863: 45).

Habitat. Lives in sandbars in large rivers and creeks in swift water.

Remarks. Elliptio c. crassidens (Lamarck) is a variable species throughout the Interior Basin, Alabama-Coosa River system, and Apalachicolan region. In the latter region, Simpson (1914, 2: 608) regarded *U. incrassatus* Lea as a variety, though he stated that, "A number of intermediate specimens from the Tennessee and Coosa rivers seem to connect the two completely." Clench and Turner (1956: 173), following Simpson, considered *incrassatus* a subspecies, but they also said, "Though the two extremes are distinct, there are all degrees of intergradation between the two forms [i.e. *crassidens* and *incrassatus*]." It is true that specimens from the Apalachicolan region are not usually as large as those from the Interior Basin, but smaller examples from both areas tend to have the characteristic radial wrinkles that extend from the posterior ridge to the posterior margin. Throughout the distribution of *E. c. crassidens*, there is a marked variation in the acuteness of the posterior ridge, the prominence of the secondary ridge and

concomitant posterior biangulation, and the breadth or acuteness of the posterior slope. There is a general tendency for the posterior ridge to be rounded and the posterior slope to be broad in specimens from the Apalachicolan region.

E. c. crassidens can be confused with some allopatric species in the Southern Atlantic Slope region, but in general, the thickness of the shell, the large, rough, pseudocardinals, and short hinge line, distinguish it from other species of *Elliptio*.

Range. Interior Basin: Mississippi drainage generally. West Gulf Coastal region, Alabama-Coosa River system, and Apalachicolan region: Amite River, Louisiana, east to the St. Marys River system, Florida. Replaced by *Elliptio fraterna* (Lea) in the Choctawhatchee River system and missing from the Ochlockonee and Suwannee river systems. Peninsular Florida: St. Petersburg, Hillsborough Co. (Pliocene).

Specimens Examined

St. Marys River System

St. Marys River Drainage. *Georgia*: St. Marys River, 2 mi. E St. George; Spanish Creek, W Folkston; St. Marys River, 4 mi. SSE Folkston; *all* Charleton Co.

Elliptio (*Elliptio*) *crassidens downiei* (Lea)

Plate 4: 1–4

Unio downici Lea 1858, Proc. Acad. Nat. Sci. Phila., 10: 166 (Buck Lake, a bayou of the Satilla River, Wayne [Brantly] Co., Georgia). Lea, 1859, Jour. Acad. Nat. Sci. Phila., ser. 2, 4: 210, pl. 25, fig. 91; figured holotype USNM 84854. Lea, 1859, Obs. Unio, 7: 28.

Unio satillaensis Lea 1858, Proc. Acad. Nat. Sci. Phila., 10: 166 (Satilla River, Camden Co., Georgia). Lea, 1859, Jour. Acad. Nat. Sci. Phila., ser. 2, 4: 216, pl. 27, fig. 96; figured holotype USNM 84855. Lea, 1859, Obs. Unio, 7: 34.

Unio spissus Lea 1859, Proc. Acad. Nat. Sci. Phila., 11: 112 (Satilla River, Wayne Co., Georgia). Lea, 1859, Jour. Acad. Nat. Sci. Phila., ser. 2, 4: 208, pl. 25, fig. 89; figured holotype USNM 84853. Lea, 1859, Obs. Unio, 7: 26.

Description. Shell large, reaching up to 100 mm in length. Outline obovate, subobovate, or rhomboid. Valves rather inflated, solid, inequilateral. Anterior end regularly rounded; posterior end broadly rounded, slightly biangulate, or truncate. Ventral margin straight or curved, sometimes rendered arcuate by slight postbasal swelling. Dorsal margin broadly rounded, forming a slight angle, occasionally a very sharp one, with the obliquely descending posterior margin. Posterior ridge varies from being rather sharp to almost imperceptible. Secondary ridge usually present. Posterior slope subtruncated to broad. Umbos rather full, but low, located in anterior fifth of shell, their sculpture consisting of a few coarse ridges running parallel to growth lines. Periostracum fine when young, yellowish or brownish with green rays, becoming dull brown or chestnut with age, varies from being clothlike to smooth and shiny.

Left valve with two heavy, rough pseudocardinal teeth, the more anterior one somewhat triangular. Hinge line short and broad, with two short, slightly curved lateral teeth. Right valve with one chunky, serrated pseudocardinal; one lateral tooth. Beak cavities very shallow, with a few dorsal muscle scars under the hinge plate. Anterior adductor muscle scars very deep, posterior ones and pallial line distinct. Nacre purplish or flesh-colored, rather dull.

Length mm	Height mm	Width mm	
95	57	42	Satilla River, 3 mi. S Hortense, Brantly Co., Georgia.
84	49	36	Buck Lake, a bayou of the Satilla River, Brantly Co., Georgia. Holotype of *U. downiei* Lea.
76	57	40	Satilla River, Wayne Co., Georgia. Holotype of *U. spissus* Lea.

Habitat. Lives in sand in swift water.

Remarks. Elliptio crassidens downiei (Lea) is quite distinct from the highly variable typical form, and has a pattern of

variability of its own, even though occasional individuals are found that are very close to some specimens from the nearby St. Marys River system. Found only in the Satilla River, *downiei* is usually considerably more inflated than the typical form. There is a tendency for the shells from the upper reaches of the river to be obovate or elongate with the posterior ridge almost imperceptible and the posterior slope very broad. Some individuals are also sometimes slightly swollen in the postbasal region. In the lower part of the river, the shells, in general, become more rhomboidal, the posterior margin appearing truncate with the posterior ridge angular and the posterior slope sharp. The posterior slope of *downiei* lacks the radial wrinkles usually present in *E. c. crassidens;* the periostracum with its satiny clothlike, or even shiny appearance, and yellowish brown to chestnut color is also distinctive.

Range. Apalachicolan region: restricted to the Satilla River system, Georgia.

Specimens Examined

Satilla River System

Satilla River Drainage. *Georgia*: Satilla River, Wayne Co. Buck Lake, a bayou of the Satilla River; Satilla River, 3 mi. S Hortense; *both* Brantly Co. Satilla River, Camden Co.

Elliptio (*Elliptio*) *congaraea* (Lea)

Plate 5: 1–8

Unio congaraeus Lea 1831, Trans. Amer. Philos. Soc., 4: 72, pl. 6, fig. 4 (Congaree River, South Carolina; figured holotype USNM 85693). Lea, 1834, Obs. Unio, 1: 82.

Unio fulvus Lea 1834, Trans. Amer. Philos. Soc., 5: 96, pl. 13, fig. 39 (South Carolina; figured holotype USNM 85679). Lea, 1834, Obs. Unio, 1: 208.

Unio lecontianus Lea 1838, Trans. Amer. Philos. Soc., 6: 40, pl. 12, fig. 35 (Canoochee River, Liberty Co., Georgia; figured holotype USNM 84852). Lea, 1838, Obs. Unio, 2: 40.

Unio planilateris Conrad 1838, Monography Unionidae, no. 11 [back cover] (Black Water River, Virginia; Neuse River; Yadkin River; *both* North Carolina). 1840, *op. cit.*, no. 12, p. 103, pl. 57, fig. 1; type from Yadkin River, not in ANSP [lost]. The specimens from the additional localities were probably *Elliptio complanata* (Lightfoot).

Unio pusillus Lea 1840, Proc. Acad. Nat. Sci. Phila., 1: 286 (Ogeechee River, Liberty Co., Georgia). Lea, 1842, Trans. Amer. Philos. Soc., 8: 220, pl. 18, fig. 36; figured holotype USNM 85241. Lea, 1842, Obs. Unio, 3: 58.

Unio sordidis Lea 1852, Trans. Amer. Philos. Soc., 10: 254, pl. 12, fig. 1 (Abbeville District [Savannah River drainage], South Carolina; figured holotype USNM 85688). Lea, 1852, Obs. Unio, 5: 10.

Unio gibbesianus Lea 1852, Trans. Amer. Philos. Soc., 10: 254, pl. 12, fig. 2 (Abbeville District [Savannah River drainage], South Carolina; figured holotype USNM 85685). Lea, 1852, Obs. Unio, 5: 10.

Unio rufusculus Lea 1852, Proc. Amer. Philos. Soc., 5: 252 (Abbeville District [Savannah River drainage], South Carolina). Lea, 1852, Trans. Amer. Philos. Soc., 10: 258, pl. 14, fig. 7; figured holotype USNM 85683. Lea, 1852, Obs. Unio, 5: 14.

Unio forbesianus Lea 1852, Proc. Amer. Philos. Soc., 5: 251 (Savannah River, Georgia). Lea, 1852, Trans. Amer. Philos. Soc., 10: 264, pl. 16, fig. 17; figured holotype USNM 84542. Lea, 1852, Obs. Unio, 5: 20.

Unio buxeus Lea 1852, Trans. Amer. Philos. Soc., 10: 261, pl. 15, fig. 13 (Abbeville District [Savannah River drainage], South Carolina; figured holotype USNM 85153). Lea, 1852, Obs. Unio, 5: 17.

Unio moussonianus Lea 1852, Trans. Amer. Philos. Soc., 10: 268, pl. 18, fig. 22 (Georgia; figured holotype USNM 85168). Lea, 1852, Obs. Unio, 5: 24.

Unio corvus Lea 1859, Proc. Acad. Nat. Sci. Phila., 11: 112 (Buckhead Creek, Burke Co.; Ogeechee River; *both* Georgia). Lea, 1859, Jour. Acad. Nat. Sci. Phila., ser. 2, 4: 217, pl. 27, fig. 97; figured holotype USNM 84539, from Buckhead Creek. Lea, 1859, Obs. Unio, 7: 35.

Unio vestitus Lea 1861, Proc. Acad. Nat. Sci. Phila., 13: 393 (Ogeechee River [Georgia]). Lea, 1862, Jour. Acad. Nat. Sci. Phila., ser. 2, 5: 189, pl. 25, fig. 259; figured holotype USNM 85332. Lea, 1862, Obs. Unio, 9: 11.

Unio dorsatus Lea 1868, Proc. Acad. Nat. Sci. Phila., 20: 160 (Catawba River, North Carolina). Lea, 1868, Jour. Acad. Nat. Sci. Phila.,

ser. 2, 6: 300, pl. 45, fig. 112; figured holotype USNM 84494. Lea, 1869, Obs. Unio, 12: 60.
Unio strumosus Lea 1872, Proc. Acad. Nat. Sci. Phila., 24: 158 (Yadkin River, North Carolina). Lea, 1874, Jour. Acad. Nat. Sci. Phila., ser. 2, 8: 57, pl. 19, fig. 55; figured holotype USNM 85755. Lea, 1874, Obs. Unio, 13: 61.

Description. Shell medium to large, reaching up to 100 mm in length. Outline long, rhomboid, subrhomboid, sometimes almost subtriangular. Valves flat to subinflated, thin to solid, inequilateral. Anterior end regularly rounded; posterior end broadly rounded, slightly biangulate or truncate. Ventral margin straight or slightly curved, occasionally a bit arcuate. Dorsal margin short to very short, forming an indistinct angle with the obliquely descending posterior margin. Posterior ridge occasionally rather sharp but more often faint to imperceptible, with the slightest hint of a secondary ridge above. Posterior slope rather broad to very broad, with numerous fine ridges that radiate from the upper posterior ridge to the dorsal margin. Umbos rather full, but low, located in the anterior third to fourth of the shell, their sculpture consisting of a few coarse ridges that run parallel to the growth lines. Periostracum smooth when young, yellowish with fine to broad green rays, sometimes becoming yellowish green but more often light brown or chestnut, generally smooth on the disk, but roughened toward the margins.

Left valve with two heavy, rough pseudocardinal teeth, the more anterior one slightly smaller and a little lower. Hinge line rather short and broad, with two short, slightly curved, granular lateral teeth, the uppermost one sometimes very short and vestigial. Right valve with one chunky, serrated pseudocardinal; one lateral tooth. Beak cavities shallow, with a few dorsal muscle scars under the hinge plate. Anterior adductor muscle scars deep, posterior ones and pallial line distinct. Nacre generally white, occasionally light pinkish or purplish.

Length mm	Height mm	Width mm	
80	48	29	Savannah River, 7 mi. NE Newington, Screven Co., Georgia.
77	40	30	As above.
70	39	24	Briar Creek, Chalker Bridge, 6 mi. N Waynesboro, Burke Co., Georgia.
51	30	18	As above.

Habitat. Lives in sand, in swift water.

Remarks. Elliptio congaraea (Lea) differs from *E. c. crassidens* of the Apalachicolan region in that the shell is less ponderous, with a tendency to be more rhomboid or subtriangular. It has a posterior ridge that is less sharp, and a broader posterior slope that is often biangulate. In some environments the posterior ridge merges imperceptibly into the posterior slope.

E. congaraea differs from *E. dariensis* (Lea). The latter has a much sharper posterior ridge, the posterior slope is more acute, with heavier sculpture, and is, in general, less often biangulate. *E. congaraea* differs from *E. crassidens downiei.* The latter is, in general, much more sharply rhomboidal and inflated.

Shells of *E. congaraea* from the Canoochee River are generally rather heavy and somewhat swollen, the posterior ridge faint and biangulate, the periostracum usually brownish yellow to chestnut and not rayed. Examples from the upper Ogeechee River tend to be moderately heavy and flat, the posterior ridge rather strong, but the preponderant form in the Ogeechee River is rather long with a faint broad biangulate posterior ridge. Shells from the Savannah River are inclined to be subtriangular with a rather sharp posterior ridge and acute posterior slope, but specimens from the tributaries tend to resemble the shells from the Ogeechee with their faint, broadly biangulate posterior ridge. The rivers to the north of the Savannah abound in the weak-ridged forms, and are often light brown or yellowish with more prominent green rays.

Range. Southern Atlantic Slope: Ogeechee River system, Georgia, north to the Cape Fear River system, North Carolina.

Specimens Examined

Ogeechee River System

Canoochee River Drainage. *Georgia*: Canoochee River, Bulloch Co. Canoochee River, Liberty Co. (USNM). Canoochee River, E Pembroke (ANSP); Canoochee River, near Clyde (MZUM); *both* Bryan Co.

Ogeechee River Drainage. *Georgia*: Ogeechee River, Shoals, 12 mi. SW Warrington, Warren Co. Ogeechee River, 4 mi. SW Mitchell, Glascock Co. Ogeechee River, 2 mi. S Louisville, Jefferson Co. Rocky Creek, 5 mi. SW Waynesboro, Burke Co. Ogeechee River, Scarboro; Ogeechee River, bridge, 1 mi. S Dover; Ogeechee River, 1.5 mi. SW Oliver; *all* Screven Co. (*all* MZUM). Ogeechee River, bridge, 1 mi. E Blitchton; Ogeechee River, Jinks Bridge, Route 16; Ogeechee River, Morgan Bridge, 14 mi. SE Pembroke; Dolly Lake, about 1.5 mi. below Kiterlighter Camp; *all* Bryan Co. (*all* MZUM).

Savannah River System

Broad River Drainage. *Georgia*: Broad River, Huguenot, Elbert Co. (USNM).

Savannah River Drainage. *Georgia*: Savannah River, Elbert Co. Savannah River, Augusta; Spirit Creek, De Bruce; *both* Richmond Co. *South Carolina*: Savannah River, 6 mi. W Martin; Savannah River, Johnsons Landing, 10 mi. W Allendale; Savannah River, King Jaw Point, 10 mi. WSW Allendale (MZUM); *all* Allendale Co. *Georgia*: Brier Creek, Chalker Bridge, 6 mi. N Waynesboro, Burke Co. Savannah River, 7 mi. NE Newington, Screven Co. *South Carolina*: Mouth of Vermezobre Creek (Savannah River Wildlife Res.) (MZUM); Savannah River at Governor Hamilton's [Mansion, 8 mi. S Hardeeville] (ANSP); *both* Jasper Co.

Edisto River System

Edisto River Drainage. *South Carolina*: Edisto River, Givhans Ferry, 2 mi. NW Givhans, Dorchester Co.

Cooper-Santee River System

Congaree River Drainage. *South Carolina*: Congaree River.

Wateree River Drainage. *North Carolina*: Catawba River, Tuckasaga Ford [not found] (ANSP). *South Carolina*: Wateree River, Camden, Kershaw Co. (MZUM).

Pedee River System

Yadkin River Drainage. *South Carolina*: Yadkin River (ANSP, USNM).

Cape Fear River System

Cape Fear River Drainage. *North Carolina*: Cape Fear River.

Elliptio (*Elliptio*) *dariensis* (Lea)

Plate 6: 1–4

Unio dariensis Lea 1842, Trans. Amer. Philos. Soc., 8: 246, pl. 26, fig. 61 ([Altamaha River] near Darien [McIntosh Co.], Georgia; figured holotype USNM 85691). Lea, 1842, Obs. Unio, 3: 84.

Unio monroensis Lea 1843, Descriptions Twelve Uniones. (Lake Monroe, Florida). Lea, 1846, Trans. Amer. Philos. Soc., 9: 279, pl. 41, fig. 8; figured holotype USNM 85169. Lea, 1848, Obs. Unio, 4: 37.

Unio websterii B. H. Wright 1888, Proc. Acad. Nat. Sci. Phila., p. 113, pl. 2, fig. 2 (Lake Woodruff, Volusia Co., Florida; lectotype USNM 125697, selected by Johnson, 1967, Occ. Pap. Moll., 3: 10, pl. 7, fig. 2).

Unio hartwrightii B. H. Wright 1896, Nautilus, 9: 121, pl. 2, figs. 4–6 (Lake Beresford [Volusia Co.], Florida; holotype USNM 151031, figured by Johnson, 1967, Occ. Pap. Moll., 3: 6, pl. 7, fig. 1 and the type locality further restricted on the basis of the original label to: [St. Johns River], Blue Springs [3 mi. S Lake Beresford, Volusia Co.], Florida).

Description. Shell often large, exceeding 130 mm in length. Outline subrhomboid or subtrapezoidal. Valves rather flat to subinflated, thin but strong, inequilateral. Anterior end regularly rounded; posterior

end occasionally a bit produced and slightly biangulate, but more often obliquely truncated. Ventral margin straight or slightly curved. Dorsal margin straight, forming a sharp angle with the obliquely descending posterior margin. Posterior ridge usually very sharp with a faint secondary ridge above. Posterior slope rather broad, but well defined, with numerous wrinkles on it. Umbos full to inflated, but rather low, located in the anterior third of the shell, their sculpture consisting of five or six double-looped bars, slightly more elevated and angular behind the sinus. Periostracum smooth when young, yellowish with fine green rays, becoming darker greenish yellow, or dark chestnut or blackish, generally smooth on the disk but sometimes roughened, especially on the posterior slope.

Left valve with two heavy, rough pseudocardinal teeth, the more anterior one slightly smaller and a little lower. Hinge line rather short and broad, with two short, slightly curved, granular, lateral teeth. Right valve with one chunky, serrated pseudocardinal; one lateral tooth. Beak cavities shallow, with a few dorsal muscle scars under the hinge plate. Anterior adductor muscle scars deep, posterior ones and pallial line distinct. Nacre generally purple, sometimes white, occasionally yellow.

Length mm	Height mm	Width mm	
130	77	47	House Creek, Bowens Mill, 9 mi. N Fitzgerald, Ben Hill Co., Georgia.
98	58	35	As above.
78	55	28	[Altamaha River], near Darien [McIntosh Co.], Georgia.
41	23	14	House Creek, Bowens Mill, 9 mi. N Fitzgerald, Ben Hill Co., Georgia.

Anatomy. Discussed by Lea (1863: 404).

Habitat. Lives in sand bars, in fast-flowing or even sluggish water.

Remarks. Elliptio dariensis (Lea) is restricted to the St. Johns River system, Florida, and the Altamaha River system, Georgia, and is close to *Elliptio c. crassidens* (Lamarck), but the shell of *dariensis* is never as ponderous; the posterior ridge is consistently much sharper, especially in immature individuals, and the posterior slope, though generally wrinkled, does not have the strong radial pattern typical of *E. c. crassidens.* Throughout its range, *dariensis* is more compressed than *E. c. downiei* (Lea) even when the posterior ridge of some individuals of both are not very acute.

Elliptio dariensis is also close to *E. congaraea* (Lea), which is found in the Ogeechee River, Georgia, to the Cape Fear River, North Carolina, but *congaraea* is more variable. It is often more rhomboid than *dariensis.* In *congaraea* the posterior ridge is less sharp, and more prone to be biangulate, resembling some examples of *E. crassidens downiei,* though the latter are more inflated. Immatures of *dariensis* tend to have a somewhat chestnut periostracum with subtle green rays, whereas *congaraea* is often quite yellow with rather bright green rays.

In the Altamaha River system, the largest specimens of *E. dariensis* are found in the lower Altamaha River. Older specimens have been confused with *E. hopetonensis* (which replaces *E. complanata* (Lightfoot) in the main river), but *hopetonensis* is proportionally longer and narrower, is without the sharp posterior ridge, and has no trace of sculpture on the posterior slope. Whereas *E. hopetonensis* is very common in the Altamaha River, *E. dariensis* is not. In a collection made by Clench, Boss and Fuller, 10 mi. NE Surrency, Appling Co., Georgia, several hundred *hopetonensis* were collected, but only three *dariensis.*

The especially sharp posterior ridge and relatively thin shell, and the similarity of the periostracum, especially as exhibited in

immatures, suggest that the forms described from the St. Johns River system are *E. dariensis*, even though the St. Johns and Altamaha river systems are separated by the St. Marys and Satilla river systems, which are inhabited by *E. c. crassidens* and *E. crassidens downiei* respectively.

Range. Peninsular Florida. St. Johns River system, Florida. Southern Atlantic Slope: Altamaha River system, Georgia.

Specimens Examined

Altamaha River System

Ocmulgee River Drainage. *Georgia*: Bozzy Branch, 4 mi. S Macon; Tobesofkee Creek, 5 mi. S Macon; *both* Bibb Co. Tucsowhatchee Creek, 5 mi. SW Hawkinsville; Cedar Creek, Fountains Mill, 7 mi. SW Hawkinsville; *both* Pulaski Co. Dicksons Creek, 10 mi. NE Fitzgerald, Ben Hill Co. Ocmulgee River, 1.5 mi. S Jacksonville; Ocmulgee River, below Lumber City, (H. D. Athearn); *both* Telfair Co.

Ohoopee River Drainage. *Georgia*: Little Ohoopee River, 1 mi. E Kite, Johnson Co. Little Ohoopee River, 11 mi. W Swainsboro; Ohoopee River, 1 mi. E Adrian; Ohoopee River, 0.5 mi. S Norristown; *all* Emanuel Co. Ohoopee River, above Reidsville, Tattnall Co.

Altamaha River Drainage. *Georgia*: Altamaha River, 10 mi. NE Surrency, Appling Co. Altamaha River, Long Co. Altamaha River, near Darien, McIntosh Co.

Elliptio (*Elliptio*) *fraterna* (Lea)

Plate 7: 1–5

Unio fraternus Lea 1852, Trans. Amer. Philos. Soc., 10: 263, pl. 16, fig. 15 ([Chattahoochee River] Columbus [Muscogee Co.], Georgia; paratype USNM 85398; Abbeville District [Savannah River drainage], South Carolina; figured holotype USNM 85396). Lea, Obs. Unio, 5: 19.

Unio anthonyi Lea 1861, Proc. Acad. Nat. Sci. Phila., 13: 41 (Florida). Lea, 1862, Jour. Acad. Nat. Sci. Phila., ser. 2, 5: 197, pl. 27, fig. 266; figured holotype USNM 84986. Lea, 1863, Obs. Unio, 9: 19.

Elliptio mcmichaeli Clench and Turner 1956, Bull. Florida State Mus., 1: 170, pl. 7, figs. 1–2 (Choctawhatchee River, 8 mi. W Miller Cross Roads, Holmes Co., Florida; holotype MCZ 191922).

Description. Shell medium to large, reaching 100 mm in length. Outline subelliptical. Valves flat, rather thin but solid, inequilateral. Anterior end regularly rounded; posterior end somewhat produced and biangulate. Ventral margin rather uniformly straight. Dorsal margin straight or slightly curved, forming an angle with the obliquely descending posterior margin. Posterior ridge fairly well defined near the umbos, becoming faint toward the posterior margin, with a second faint ridge above, ending in a slight biangulation. Posterior slope slightly concave and broad, often sculptured toward the umbos with wrinkles that radiate from the posterior ridge to the dorsal margin. Umbos full but low, located in the anterior fourth of the shell. Periostracum smooth and shiny on the disk, light brownish, reddish brown, or yellowish, often with fine green rays when young, becoming uniformly brownish with age.

Left valve with two heavy, rough pseudocardinal teeth, the more anterior one smaller and lower. Hinge line very short and rather narrow; two rather long slightly curved lateral teeth. Right valve with one chunky, serrated pseudocardinal; one lateral tooth. Beak cavities very shallow, with a few dorsal muscle scars under the hinge plate. Anterior adductor muscle scars deep, posterior ones and pallial line distinct. Nacre usually white, sometimes pale pink to salmon, or purplish, especially toward the edges, iridescent posteriorly.

Length mm	Height mm	Width mm	
65	30	20	Abbeville District, South Carolina.
60	31	16	As above. Holotype of *U. fraternus* Lea.
50	27	17	As above.

Anatomy. Discussed by Lea (1863: 410).

Habitat. Lives in sand bars in large rivers and their smaller tributaries, in swift water.

Remarks. Elliptio fraterna (Lea) of the Choctawhatchee River system replaces the widely distributed *E. c. crassidens* (Lamarck) which is found in both river systems adjacent to the Choctawhatchee. It is obviously close to *crassidens*, but the shell of *fraterna* is lighter, the outline is subelliptical, and the shell is consistently more elongated and compressed. The posterior ridge is less acute and the posterior slope is broader. In the Atlantic drainage, *fraterna* resembles some forms of *E. crassidens downiei* and *E. congaraea*, but the shell of *fraterna* is consistently thinner and more compressed.

The discontinuous distribution of populations of *fraterna* was used as a reason for establishing *mcmichaeli* by Clench and Turner (1956: 171). In the United States National Museum are specimens from the Chattahoochee River, Columbus, Muscogee Co., Georgia. This locality is near the headwaters of the Choctawhatchee River system, and it is likely that *fraterna* spread into the Chattahoochee River in this vicinity, as is suggested here in Chapter 1. Further, commingling of the waters of the upper Chattahoochee and Savannah rivers is attested to by a number of species common to both drainages, besides *fraterna*.

Clench and Turner claim that *mcmichaeli* is larger than *fraterna* and that occasional specimens, "show salmon coloration [nacre]," but a comparison of the holotypes and all available series indicate that the specimens can not be distinguished morphologically.

Range. Apalachicolan region: restricted to the Choctawhatchee River system, Florida, and the upper Chattahoochee River, Georgia, of the Apalachicola River system. Southern Atlantic Slope: upper Savannah River system, South Carolina.

Specimens Examined

Savannah River System

Savannah River Drainage. *South Carolina:* Abbeville District (USNM).

Elliptio (*Elliptio*) *waccamawensis* (Lea)

Plate 7: 6, 7

Unio waccamawensis Lea 1863, Proc. Acad. Nat. Sci. Phila., 15: 193 (Lake Waccamaw, North Carolina). Lea, 1866, Jour. Acad. Nat. Sci. Phila., ser. 2, 6: 16, pl. 5, fig. 14: figured holotype USNM 84437. Lea, 1867, Obs. Unio, 11: 20. Simpson, 1914, Cat. Naiades, 2:620.

Description. Shell generally small, not reaching more than 60 mm, though occasionally reaching almost 90 mm in length. Outline elongated rhomboid. Valves inflated or subinflated, thin, inequilateral. Anterior end regularly rounded; posterior end slightly biangulate and pointed toward the base. Ventral margin quite straight. Dorsal margin rather short and straight, meeting the obliquely descending posterior margin in a usually distinct angle. Hinge ligament long and low. Posterior ridge very high, decidedly angular, with sometimes a faint second ridge above it ending behind in a broad point. Posterior slope obliquely truncate, often with wrinkled sculpture. Umbos neither high nor full, located in the anterior quarter of the shell, their sculpture not observed. Periostracum rather smooth, with delicate growth lines, generally smoky-green, sometimes yellowish or brownish, often with dark green rays over the entire surface.

Left valve with two, occasionally three, stumpy pseudocardinal teeth, one in front of the other, often of almost equal height. Hinge line very short and narrow, two rather short straight lateral teeth. Right valve with two parallel pseudocardinals, the posterior one inclined to be narrow and triangular, occasionally broken into two teeth, the more anterior tooth low and vestigial; one lateral tooth. Beak cavities very shallow, with a few dorsal muscle scars. Anterior and posterior adductor

muscle scars and pallial line distinct. Nacre generally bluish white or pink, sometimes yellowish, somewhat iridescent.

Length mm	Height mm	Width mm	
88	45	28	A drainage canal, 1 mi. NNW Dupree Landing, Columbus Co., North Carolina.
61	34	22	As above.
54	32	22	Lake Waccamaw, [town of] Lake Waccamaw, Columbus Co., North Carolina.

Habitat. Lives in sand, in sluggish water.

Remarks. Elliptio waccamawensis (Lea), which is restricted to the Waccamaw River system, most closely resembles *E. congaraea* (Lea) from the nearby Cape Fear River system, though *waccamawensis* is easily distinguished from it by being consistently more elongated, with a decidedly more acutely angled posterior ridge. In both species, the posterior slope has the tendency to have wrinkled sculpture, but the periostracum of *waccamawensis* tends to be more intensely green and is more inclined to be rayed.

Specimens of unionids from Lake Waccamaw have always been greatly corroded and many of their conchological characters obfuscated, but recently H. D. Athearn has taken some more perfect examples of *waccamawensis* from the obviously hospitable environment of a canal that was dug parallel to the road on the west side of the lake.

Range. Southern Atlantic Slope: restricted to the Waccamaw River system, North Carolina.

Specimens Examined

Waccamaw River System

Waccamaw River Drainage. *North Carolina:* Lake Waccamaw, [town of] Lake Waccamaw; Lake Waccamaw, 0.5 mi. W [town of] Lake Waccamaw; Drainage canal, beside Lake Waccamaw, 1 mi. NNW Dupree Landing; *all* Columbus Co.

Elliptio (*Elliptio*) *complanata* (Lightfoot)

Plate 8: 1–6

Mya complanata (Lightfoot) 1786, Catalogue of the Portland Museum, p. 100, no. 2190 (Maryland) refers to: Lister, 1686, Synopsis Methodicae Conchyliorum, pl. 150, fig. 5 (Virginia; figured specimen Oxford Univ. Mus. [probably lost] *teste* Dance, 1966, Shell Collecting, p. 292). Type locality restricted to the Potomac River, Washington, District of Columbia [approximately opposite Fairfax Co., Virginia] by Johnson, 1948, Nautilus, 62: 36. In citing Lightfoot rather than Solander (Johnson *loc. cit.*) as the authority for this species I have followed Rehder (1967: 2, 18).

Unio violaceus Spengler 1793, Skrivter af Naturhistorie Selskabet [Copenhagen], 3: 55 (Nordamerika; holotype, Copenhagen Museum; figured by Haas, 1913, Vidensk. Meddr. Dansk Naturh. Foren. [Copenhagen], 65: 51, text fig.).

Unio purpureus Say 1817, Nicholson's Encyclopedia, 2 [no pagination], pl. 3, fig. 1 (Delaware and Schuylkill Rivers [presumably near Philadelphia, Philadelphia Co., Pennsylvania], type, ANSP [lost]).

Unio rarisulcata Lamarck 1819, Hist. Nat. des Animaux sans Vertèbres, 6 (1): 72 (le lac Champlain [Vermont]; type, Cab. of M. Dufresne [lost]).

Unio coarctata Lamarck 1819, Hist. Nat. des Animaux sans Vertèbres, 6 (1): 73 (la rivière Hudson [New York]; holotype, Paris Museum, figured by Johnson, 1969, Nautilus, 83: 53, fig. 5).

Unio purpurascens Lamarck 1819, Hist. Nat. des Animaux sans Vertèbres, 6 (1): 73 (les rivières de l'etat de New Yorck [*sic*]; type, Cab. of M. Valenciennes [lost]; type of var. b and c, Paris Museum, the latter selected as lectotype by Johnson, 1969, Nautilus, 83: 60, fig. 6 du lac Champlain [New York]).

Unio rhombula Lamarck 1819, Hist. Nat. des Animaux sans Vertèbres, 6 (1): 74 (Sénégal; [erroneous] holotype, Geneva Museum, figured by Delessert, 1841, Rec. Coq. de Lamarck, pl. 12, fig. 8).

Unio carinifera Lamarck 1819, Hist. Nat. des Animaux sans Vertèbres, 6 (1): 74 (la rivière Hudson de l'etat de New York; holotype, Paris Museum, figured by Johnson, 1969, Nautilus, 83: 52, fig. 4).

Unio georgina Lamarck 1819, Hist. Nat. des Animaux sans Vertèbres, 6 (1): 74 (le lac George [New York]; holotype, Paris Museum,

figured by Johnson, 1969, Nautilus, 83: 53, fig. 3).

Unio glabrata Lamarck 1819, Hist. Nat. des Animaux sans Vertèbres, 6 (1): 75 (la rivière de l'Ohio; [erroneous] holotype, Paris Museum, figured by Johnson, 1969, Nautilus, 83: 53, fig. 7).

Unio sulcideus Lamarck 1819, Hist. Nat. des Animaux sans Vertèbres, 6 (1): 77 (une rivière du Connecticut; holotype, Paris Museum, Schunglkill [Schuylkill River], Pennsylvania; paratype, Geneva Museum, figured by Delessert, 1841, Rec. Coq. de Lamarck, pl. 12, fig. 3.

Unio virginiana Lamarck 1819, Hist. Nat. des Animaux sans Vertèbres, 6 (1): 79 (la rivière Potowmac [Potomac] en Virginie; holotype, Geneva Museum, figured by Delessert, 1841, Rec. Coq. de Lamarck, pl. 12, fig. 4.

Unio aurata Rafinesque 1820, Ann. Gén. Sci. Phys. (Bruxelles), 5: 295 (la rivière Hudson [New York]; type not in ANSP [lost]).

Unio fluviatilis Green 1827, Jour. Machurian Lyceum (Philadelphia), 1: 41. [no locality; type lost.]

Mya rigida Wood 1828, Index Testaceologicus, Supplement, pl. 1, fig. 10 (no locality; type [lost]). Wood, 1856, *op. cit.*, ed. Hanley, p. 200, pl. 1, supp. fig. 10.

Unio griffithianus Lea 1834, Trans. Amer. Philos. Soc., 5: 103, pl. 15, fig. 46 (South Carolina; figured holotype USNM 85610). Lea, 1834, Obs. Unio, 1: 215.

Unio complanatus subinflatus Conrad 1835, New Fresh Water Shells United States, Appendix, p. 5, pl. 9, fig. 2 (Savannah River [Augusta, Richmond Co., Georgia]; syntype ANSP 119985; and Congaree River, South Carolina). Conrad, 1838, Monography Unionidae, no. 11, p. 97, pl. 54, fig. 1.

Unio jejunus Lea 1838, Trans. Amer. Philos. Soc., 6: 9, pl. 4, fig. 9 (Roanoke River [road between Winton and Tarborough, North Carolina]); [Wateree River], near Camden, [Kershaw Co.], South Carolina, figured holotype USNM 85475. Lea, 1838, Obs. Unio, 2: 9.

Unio roanokensis Lea 1838, Trans. Amer. Philos. Soc., 6: 27, pl. 8, fig. 21 (Roanoke River [road between Norfolk, Virginia; and Tarborough, North Carolina] figured holotype USNM 85423; Altamaha [River], Georgia). Lea, 1838, Obs. Unio, 2: 27.

Unio fuliginosus Lea 1845, Proc. Amer. Philos. Soc., 4: 164 (Cobb's Creek, near Philadelphia [Philadelphia Co.], Pennsylvania). Lea, 1848, Trans. Amer. Philos. Soc., 10: 78, pl. 7, fig. 19; figured holotype USNM 85665. Lea, 1848, Obs. Unio, 4: 52.

Unio cuvierianus Lea 1852, Trans. Amer. Philos. Soc., 19: 263, pl. 16, fig. 16 (Washington Co., Georgia; figured holotype USNM 85401). Lea, 1852, Obs. Unio, 5: 19.

Unio errans Lea 1856, Proc. Acad. Nat. Sci. Phila., 8: 262 (Tobesaufke [Tobesofkee] Creek, near Macon [Bibb Co.], Georgia). Lea, 1858, Jour. Acad. Nat. Sci. Phila., ser. 2, 4: 60, pl. 9, fig. 42; figured holotype USNM 85541. Lea, 1858, Obs. Unio, 6: 60.

Unio vicinus Lea 1856, Proc. Acad. Nat. Sci. Phila., 8: 262 (Swift Creek, near Macon [Bibb Co.], Georgia). Lea, 1858, Jour. Acad. Nat. Sci. Phila., ser. 2, 4: 61, pl. 9, fig. 43; figured holotype USNM 85543. Lea, 1858, Obs. Unio, 6: 61.

Unio geminus Lea 1856, Proc. Acad. Nat. Sci. Phila., 8: 262 (Buckhead Creek, Burke Co., Georgia). Lea, 1858, Jour. Acad. Nat. Sci. Phila., ser. 2, 4: 63, pl. 10, fig. 45; figured holotype USNM 84856. Lea, 1858, Obs. Unio, 6: 63.

Unio abbevillensis Lea 1857, Proc. Acad. Nat. Sci. Phila., 9: 84 (Abbeville District [Savannah River drainage], South Carolina). Lea, 1857, Jour. Acad. Nat. Sci. Phila., ser. 2, 4: 51, pl. 6, fig. 34; figured holotype USNM 85583. Lea, 1858, Obs. Unio, 6: 51.

Unio percoarctatus Lea 1857, Proc. Acad. Nat. Sci. Phila., 9: 85 (Catawba River, Gaston Co., North Carolina). Lea, 1862, Jour. Acad. Nat. Sci. Phila., ser. 2, 5: 59, pl. 3, fig. 206; figured holotype USNM 85529. Lea, 1862, Obs. Unio, 8: 63.

Unio wheatleyi Lea 1857, Proc. Acad. Nat. Sci. Phila., 9: 85 (Catawba River, Gaston Co., North Carolina). Erroneously thought preoccupied by Lea and changed to:

Unio catawbensis Lea 1861, Jour. Acad. Nat. Sci. Phila., ser. 2, 5: 54, pl. 1, fig. 200; figured holotype USNM 85547. Lea, 1861, Obs. Unio, 8: 58.

Unio insulsus Lea 1857, Proc. Acad. Nat. Sci. Phila., 9: 86 (Roanoke River, Weldon [Halifax Co.], North Carolina). Lea, 1862, Jour. Acad. Nat. Sci. Phila., ser. 2, 5: 53, pl. 1, fig. 199; figured holotype USNM 85644. Lea, 1862, Obs. Unio, 8: 57.

Unio spadiceus Lea 1857, Proc. Acad. Nat. Sci. Phila., 9: 86 (Deep River, Gulf [Chatham Co.]; mountain streams; *both* North Carolina). Lea, 1862, Jour. Acad. Nat. Sci. Phila., ser. 2, 5: 55, pl. 1, fig. 201; figured holotype USNM 85251, from mountain streams, North Carolina. Lea, 1862, Obs. Unio, 8: 59.

Unio macer Lea 1857, Proc. Acad. Nat. Sci. Phila., 9: 86 (Roanoke River, Weldon [Halifax Co.], North Carolina). Lea, 1862, Jour. Acad. Nat. Sci. Phila., ser. 2, 5: 202, pl. 29, fig. 271;

figured holotype USNM 85427, labeled; Neuse River, near Raleigh [Wake Co.], North Carolina. Lea, 1863, Obs. Unio, 9: 24.

Unio contractus Lea 1857, Proc. Acad. Nat. Sci. Phila., 9: 86 (Roanoke River, Weldon [Halifax Co.], North Carolina). Lea, 1862, Jour. Acad. Nat. Sci. Phila., ser. 2, 5: 203, pl. 29, fig. 272: figured holotype USNM 86102. Lea, 1862, Obs. Unio, 9: 25.

Unio virens Lea 1857, Proc. Acad. Nat. Sci. Phila., 9: 169 (Georgia). Lea, 1858, Jour. Acad. Nat. Sci. Phila., ser. 2, 4: 80, pl. 16, fig. 60; figured holotype USNM 85544. Lea, 1858, Obs. Unio, 6: 80.

Unio savannahensis Lea 1857, Proc. Acad. Nat. Sci. Phila., 9: 169 (Savannah River, Brantley's Mill [not located], Washington Co., *both* Georgia; Santee Canal, South Carolina; Sugar Creek, Mecklenburg Co., North Carolina). Lea, 1858, Jour. Acad. Nat. Sci. Phila., ser. 2, 4: 80, pl. 16, fig. 61; figured holotype USNM 85404 from Savannah River. Lea, 1858, Obs. Unio, 6: 81.

Unio subflavus Lea 1857, Proc. Acad. Nat. Sci. Phila., 9: 170 (Walnut Creek above Macon [Bibb Co.], Georgia); Lea, 1858, Jour. Acad. Nat. Sci. Phila., ser. 2, 4: 90, pl. 19, fig. 70; figured holotype USNM 85562. Lea, 1858, Obs. Unio, 6: 90.

Unio fumatus Lea 1857, Proc. Acad. Nat. Sci. Phila., 9: 171 (Chattahoochee River, near Columbus [Muscogee Co.], Georgia; Hospaliga Creek, Alabama, [and] Georgia). Lea, 1858, Jour. Acad. Nat. Sci. Phila., ser. 2, 4: 88, pl. 18, fig. 68; figured holotype USNM 85552, from Chattahoochee River. Lea, 1858, Obs. Unio, 6: 88.

Unio subniger Lea 1857, Proc. Acad. Nat. Sci. Phila., 9: 172 (Flint River, near Macon [County], Georgia). Lea, 1859, Jour. Acad. Nat. Sci. Phila., ser. 2, 4: 196, pl. 22, fig. 79; figured holotype USNM 85560. Lea, 1859, Obs. Unio, 7: 14.

Unio neusensis Lea 1858, Proc. Acad. Nat. Sci. Phila., 10: 41 (Neuse River, 6 miles from [East] Raleigh [Wake Co.], North Carolina). Lea, 1859, Jour. Acad. Nat. Sci. Phila., ser. 2, 5: 60, pl. 4, fig. 208; figured holotype USNM 85465. Lea, 1860, Obs. Unio, 8: 64.

Unio purus Lea 1858, Proc. Acad. Nat. Sci. Phila., 10: 41 (Neuse River, 6 miles from [East] Raleigh [Wake Co.], North Carolina). Lea, 1859, Jour. Acad. Nat. Sci. Phila., ser. 2, 5: 61, pl. 4, fig. 209; figured holotype USNM 85003. Lea, 1860, Obs. Unio, 8: 65.

Unio exactus Lea 1858, Proc. Acad. Nat. Sci. Phila., 10: 41 (Neuse River, 6 miles from [East] Raleigh [Wake Co.], North Carolina). Lea, 1859, Jour. Acad. Nat. Sci. Phila., ser. 2, 5: 62, pl. 4, fig. 210; figured holotype USNM 85002. Lea, 1860, Obs. Unio, 8: 66.

Unio postellii Lea 1858, Proc. Acad. Nat. Sci. Phila., 10: 165 (Randall's Creek, near Columbus [Muscogee Co.]; Carter's Creek, Baldwin Co.; *both* Georgia). Lea, 1859, Jour. Acad. Nat. Sci. Phila., ser. 2, 4: 214, pl. 26, fig. 94; figured holotype USNM 85470 from Carter's Creek. Lea, 1859, Obs. Unio, 7: 32.

Unio roswellensis Lea 1858, Proc. Acad. Nat. Sci. Phila., 10: 165 (Chattahoochee River, Roswell, Cobb Co., Georgia). Lea, 1859, Jour. Acad. Nat. Sci. Phila., ser. 2, 4: 205, pl. 24, fig. 87; figured holotype USNM 85467. Lea, 1859, Obs. Unio, 7: 23.

Unio burkensis Lea 1859, Proc. Acad. Nat. Sci. Phila., 11: 112 (Buckhead Creek, Burke Co., Georgia). Lea, 1859, Jour. Acad. Nat. Sci. Phila., ser. 2, 4: 215, pl. 27, fig. 95; figured holotype USNM 85998. Lea, 1859, Obs. Unio, 7: 33.

Unio hallenbeckii Lea 1859, Proc. Acad. Nat. Sci. Phila., 11: 170 (Flat Rock Creek; Four Mile Creek; *both* near Columbus [Muscogee Co.], Georgia). Lea, 1860, Jour. Acad. Nat. Sci. Phila., ser. 2, 4: 328, pl. 51, fig. 154; figured holotype USNM 85537, from Black Dirt Creek, near Columbus [Muscogee Co.], Georgia. Lea, 1860, Obs. Unio, 8: 10.

Unio baldwinensis Lea 1859, Proc. Acad. Nat. Sci. Phila., 11: 170 (Carter's Creek, Baldwin Co., Georgia). Lea, 1860, Jour. Acad. Nat. Sci. Phila., ser. 2, 4: 330, pl. 51, fig. 155; figured holotype USNM 85420. Lea, 1860, Obs. Unio, 8: 12.

Unio salebrosus Lea 1859, Proc. Acad. Nat. Sci. Phila., 11: 170 (Flat Rock Creek; Bull Creek; Chattahoochee River; *all* near Columbus [Muscogee Co.], Georgia). Lea, 1860, Jour. Acad. Nat. Sci. Phila., ser. 2, 4: 332, pl. 52, fig. 157; figured holotype USNM 85574, from Flat Rock Creek. Lea, 1860, Obs. Unio, 8: 14.

Unio raeensis Lea 1859, Proc. Acad. Nat. Sci. Phila., 11: 171 (Chattahoochee [River], near Columbus [Muscogee Co.] and Rae's Creek [not located], Georgia). Lea, 1860, Jour. Acad. Nat. Sci. Phila., ser. 2, 4: 331, pl. 52, fig. 156; figured holotype USNM 85571. Lea, 1860, Obs. Unio, 8: 13.

Unio latus Lea 1859, Proc. Acad. Nat. Sci. Phila., 11: 171 (Savannah River, near Savannah [Chatham Co.], Georgia). Lea, 1860, Jour. Acad. Nat. Sci. Phila., ser. 2, 4: 334, pl. 53, fig. 159; figured holotype USNM 85898. Lea, 1860, Obs. Unio, 8: 16.

Unio quadratus Lea 1859, Proc. Acad. Nat. Sci. Phila., 11: 172 (Carter's Creek, [Baldwin Co.]; Factory Creek, near Columbus [Muscogee Co.]; *both* Georgia). Lea, 1860, Jour. Acad. Nat.

Sci. Phila., ser. 2, 4: 338, pl. 54, fig. 163; figured holotype USNM 85718 from Factory Creek. Lea, 1860, Obs. Unio, 8: 20.

Unio squameus Lea 1861, Proc. Acad. Nat. Sci. Phila., 13: 391 (North Carolina). Lea, 1862, Jour. Acad. Nat. Sci. Phila., ser. 2, 5: 200, pl. 28, fig. 269; figured holotype USNM 85530. Lea, 1863, Obs. Unio, 9: 22.

Unio rostrum Lea 1861, Proc. Acad. Nat. Sci. Phila., 13: 391 (Davidson Co., North Carolina). Lea, 1862, Jour. Acad. Nat. Sci. Phila., ser. 2, 5: 201, pl. 29, fig. 270; figured holotype USNM 85556. Lea, 1863, Obs. Unio, 9: 23.

Unio northamptonensis Lea 1861, Proc. Acad. Nat. Sci. Phila., 13: 392 (Connecticut River, Northampton [Hampshire Co.]; [Connecticut River] Springfield [Hampden Co.]; *both* Massachusetts. [Connecticut River] below Hartford [Hartford Co.], Connecticut; Neuse River, North Carolina). Lea, 1862, Jour. Acad. Nat. Sci. Phila., ser. 2, 5: 190, pl. 25, fig. 260; figured holotype USNM 85527 from the Connecticut River, Northampton [Hampshire Co.], Massachusetts. Lea, 1863, Obs. Unio, 9: 12.

Unio decumbens Lea 1861, Proc. Acad. Nat. Sci. Phila., 14: 40 (Alabama). Lea, 1862, Jour. Acad. Nat. Sci. Phila., ser. 2, 5: 87, pl. 12, fig. 236; figured holotype USNM 86150 [not seen]. Lea, 1862, Obs. Unio, 8: 91. Is *E. complanata, fide* Frierson, 1922, Nautilus, 36: 44.

Unio raleighensis Lea 1863, Proc. Acad. Nat. Sci. Phila., 15: 191 (Neuse River, 6 mi. East of Raleigh [Wake Co.], North Carolina). Lea, 1866, Jour. Acad. Nat. Sci. Phila., ser. 2, 6: 6, pl. 1, fig. 2; figured holotype USNM 85592. Lea, 1867, Obs. Unio, 11: 10.

Unio aberrans Lea 1863, Proc. Acad. Nat. Sci. Phila., 15: 191 (Neuse River, 6 mi. East of Raleigh [Wake Co.], North Carolina). Lea, 1866, Jour. Acad. Nat. Sci. Phila., ser. 2, 6: 7, pl. 1, fig. 3, figured holotype USNM 85600. Lea, 1867, Obs. Unio, 11: 1.

Unio weldonensis Lea 1863, Proc. Acad. Nat. Sci. Phila., 15: 191 (Roanoke River, Weldon [Halifax Co.], North Carolina). Lea, 1866, Jour. Acad. Nat. Sci. Phila., ser. 2, 6: 11, pl. 3, fig. 8; figured holotype USNM 85407. Lea, 1867, Obs. Unio, 11: 15.

Unio mecklenbergensis Lea 1863, Proc. Acad. Nat. Sci. Phila., 15: 191 (near Charlotte, Mecklenberg [*sic*] Co., North Carolina). Lea, 1866, Jour. Acad. Nat. Sci. Phila., ser. 2, 6: 17, pl. 5, fig. 15, figured holotype USNM 85419. Lea, 1867, Obs. Unio, 11: 21.

Unio chathamensis Lea 1863, Proc. Acad. Nat. Sci. Phila., 15: 191 (Rocky Run, Chatham Co., North Carolina; James River, near Richmond [Henrico Co.], Virginia). Lea, 1866, Jour. Acad. Nat. Sci. Phila., ser. 2, 6: 21, pl. 6, fig. 19; figured holotype USNM 85672 from Rocky Run. Lea, 1867, Obs. Unio, 11: 25.

Unio gastonensis Lea 1863, Proc. Acad. Nat. Sci. Phila., 15: 191 (Mine Creek, Gaston Co., North Carolina). Lea, 1866, Jour. Acad. Nat. Sci. Phila., ser. 2, 6: 20, pl. 6, fig. 18; figured holotype USNM 85409. Lea, 1867, Obs. Unio, 11: 24.

Unio quadrilaterus Lea 1863, Proc. Acad. Nat. Sci. Phila., 15: 192 (Abbeville District [Savannah River drainage], South Carolina; Neuse River, near [6 miles East of] Raleigh [Wake Co.]; Catawba River; *both* North Carolina). Lea, 1866, Jour. Acad. Nat. Sci. Phila., ser. 2, 6: 5, pl. 1, fig. 1; figured holotype USNM 85385 from the Neuse River. Lea, 1867, Obs. Unio, 11: 9.

Unio indefinitus Lea 1863, Proc. Acad. Nat. Sci. Phila., 15: 192 (Long Creek, Mecklenburg Co.; Neuse River, near [6 miles East of] Raleigh [Wake Co.]; *both* North Carolina). Changed to:

Unio indefinitus Lea 1866, Jour. Acad. Nat. Sci. Phila., ser. 2, 6: 15, pl. 4, fig. 12; figured holotype USNM 85388, from Long Creek. Lea, 1867, Obs. Unio, 11: 19.

Unio cistelliformis Lea 1863, Proc. Acad. Nat. Sci. Phila., 15: 192 (Neuse River, near [6 miles East of] Raleigh [Wake Co.], North Carolina). Lea, 1866, Jour. Acad. Nat. Sci. Phila., ser. 2, 6: 19, pl. 6, fig. 17; figured holotype USNM 85533. Lea, 1867, Obs. Unio, 11: 23.

Unio mediocris Lea 1863, Proc. Acad. Nat. Sci. Phila., 15: 192 (Neuse River, [6 miles East of] Raleigh [Wake Co.], North Carolina). Lea, 1866, Jour. Acad. Nat. Sci. Phila., ser. 2, 6: 24, pl. 7, fig. 22; figured holotype USNM 85611. Lea, 1866, Obs. Unio, 11: 28.

Unio perluccns Lea 1863, Proc. Acad. Nat. Sci. Phila., 15: 193 (Six Runs, Sampson Co., North Carolina). Lea, 1866, Jour. Acad. Nat. Sci. Phila., ser. 2, 6: 18, pl. 5, fig. 16; figured holotype USNM 85076. Lea, 1867, Obs. Unio, 11: 22.

Unio curatus Lea 1863, Proc. Acad. Nat. Sci. Phila., 15: 193 (Sugar Creek [Mecklenburg Co.], North Carolina). Lea, 1866, Jour. Acad. Nat. Sci. Phila., ser. 2, 6: 23, pl. 7, fig. 21; type, C. M. Wheatley collection in ANSP; the only specimen located, ANSP 127200, is not figured type. Lea, 1867, Obs. Unio, 11: 27.

Unio protensus Lea 1865, Proc. Acad. Nat. Sci. Phila., 17: 33 (North Carolina). Lea, 1868, Jour. Acad. Nat. Sci. Phila., ser. 2, 6: 256, pl. 31, fig. 71; figured holotype USNM 85994, from Eno River, near Hillsboro, Orange Co., North Carolina. Lea, 1868, Obs. Unio, 12: 16.

Unio lazarus Sowerby 1868 *in* Reeve, Conch. Iconica 16, *Unio,* pl. 68, fig. 348 (Abbeville

District [Savannah River drainage], South Carolina) *non* Lea, 1852.

Unio beaverensis Lea 1868, Proc. Acad. Nat. Sci. Phila., 20: 161 (Beaver Creek [Gaston Co.]; Long Creek [Gaston Co.]; *both* North Carolina. Carter's Creek [Baldwin Co.], Georgia). Lea, 1868, Jour. Acad. Nat. Sci. Phila., ser. 2, 6: 297, pl. 44, fig. 109; figured holotype USNM 85598 from Beaver Creek. Lea, 1869, Obs. Unio, 12: 57.

Unio nubilus Lea 1868, Proc. Acad. Nat. Sci. Phila., 20: 161 (Paw Creek, Mecklenburg Co., North Carolina). Lea, 1868, Jour. Acad. Nat. Sci. Phila., ser. 2, 6: 298, pl. 44, fig. 110; figured holotype USNM 85417. Lea, 1869, Obs. Unio, 12: 58.

Unio datus Lea 1868, Proc. Acad. Nat. Sci. Phila., 20: 161 (Paw Creek [Mecklenburg Co.]; Beaver Co. [= Creek, Gaston Co.]; Long Creek [Gaston Co.]; *all* North Carolina). Lea, 1868, Jour. Acad. Nat. Sci. Phila., ser. 2, 6: 299, pl. 44, fig. 111; figured holotype USNM 85097 labeled, "Paw Creek, Beaver Co., North Carolina." Lea, 1869, Obs. Unio, 12: 59.

Unio humerosus Lea 1868, Proc. Acad. Nat. Sci. Phila., 20: 161 (Charlotte, Mecklenburg Co., North Carolina). Lea, 1868, Jour. Acad. Nat. Sci. Phila., ser. 2, 6: 301, pl. 45, fig. 113; figured holotype USNM 85414. Lea, 1869, Obs. Unio, 12: 61.

Unio uhareensis Lea 1868, Proc. Acad. Nat. Sci. Phila., 20: 145 (Uharee [Uwharree] River, Montgomery Co., North Carolina). Lea, 1868, Jour. Acad. Nat. Sci. Phila., ser. 2, 6: 304, pl. 46, fig. 116; figured holotype USNM 85576. Lea, 1869, Obs. Unio, 12: 63.

Unio tortuosus Sowerby 1868, Conch. Iconica, 16, *Unio*, pl. 65, fig. 330 (Maryland; figured holotype BMNH 74.12.11.25).

Unio santeensis Lea 1871, Proc. Acad. Nat. Sci. Phila., 23: 193 (Santee Canal, South Carolina; Oconee River, Georgia). Lea, 1874, Jour. Acad. Nat. Sci. Phila., ser. 2, 8: 20, pl. 6, fig. 17; figured holotype USNM 85635, from Santee Canal. Lea, 1874, Obs. Unio, 13: 24.

Unio yadkinensis Lea 1872, Proc. Acad. Nat. Sci. Phila., 24: 156 (Yadkin River, near Salisbury [Rowan Co.], North Carolina). Lea, 1874, Jour. Acad. Nat. Sci. Phila., ser. 2, 8: 32, pl. 10, fig. 29; figured holotype USNM 85387. Lea, 1874, Obs. Unio, 13: 36.

Unio amplus Lea 1872, Proc. Acad. Nat. Sci. Phila., 24: 157 (Irwin's Creek, Mecklenburg Co., North Carolina). Lea, 1874, Jour. Acad. Nat. Sci. Phila., ser. 2, 8: 39, pl. 13, fig. 36; figured holotype USNM 85591. Lea, 1874, Obs. Unio, 13: 43.

Unio ligatus Lea 1872, Proc. Acad. Nat. Sci. Phila., 24: 157 (Irwin's Creek, Mecklenburg Co.; Long Creek, Gaston Co.; *both* North Carolina). Lea, 1874, Jour. Acad. Nat. Sci. Phila., ser. 2, 8: 49, pl. 17, fig. 47; figured holotype USNM 85590, from Irwin's Creek. Lea, 1874, Obs. Unio, 13: 53.

Unio differtus Lea 1872, Proc. Acad. Nat. Sci. Phila., 24: 158 ([Savannah River], Georgia ?). Lea, 1874, Jour. Acad. Nat. Sci. Phila., ser. 2, 8: 42, pl. 14, fig. 39; figured holotype USNM 85399. Lea, 1874, Obs. Unio, 13: 46.

Unio subparallelus Lea 1872, Proc. Acad. Nat. Sci. Phila., 24: 158 (Irwin's Creek [Mecklenburg Co.]; Fox River [not located]; *both* North Carolina). Lea, 1874, Jour. Acad. Nat. Sci. Phila., ser. 2, 8: 46, pl. 16, fig. 44; figured holotype USNM 85418, localities not separated. Lea, 1874, Obs. Unio, 13: 50.

Unio oblongus Lea 1872, Proc. Acad. Nat. Sci. Phila., 24: 158 (Irwin's Creek, Mecklenburg Co., North Carolina). Lea, 1874, Jour. Acad. Nat. Sci. Phila., ser. 2, 8: 52, pl. 18, fig. 50; figured holotype USNM 85572. Lea, 1874, Obs. Unio, 13: 56.

Unio curvatus Lea 1872, Proc. Acad. Nat. Sci. Phila., 24: 159 (Pfeiffers Pond [Charlotte], Mecklenburg Co., North Carolina). Lea, 1874, Jour. Acad. Nat. Sci. Phila., ser. 2, 8: 47, pl. 13, fig. 35; figured holotype USNM 85550. Lea, 1874, Obs. Unio, 13: 42.

Unio irwinensis Lea 1872, Proc. Acad. Nat. Sci. Phila., 24: 159 (Irwin's Creek, [Mecklenburg Co.], North Carolina). Lea, 1874, Jour. Acad. Nat. Sci. Phila., ser. 2, 8: 44, pl. 15, fig. 42; figured holotype USNM 85680. Lea, 1874, Obs. Unio, 13: 48.

Unio subsquamosus Lea 1872, Proc. Acad. Nat. Sci. Phila., 24: 160 (Yadkin River, North Carolina). Lea, 1874, Jour. Acad. Nat. Sci. Phila., ser. 2, 8: 47, pl. 16, fig. 45; figured holotype USNM 85557. Lea, 1874, Obs. Unio, 13: 51.

Unio infuscus Lea 1872, Proc. Acad. Nat. Sci. Phila., 24: 160 (Fox River [not located]; Irwin's Creek, Mecklenburg Co.; *both* North Carolina). Lea, 1874, Jour. Acad. Nat. Sci. Phila., ser. 2, 8: 51, pl. 17, fig. 49; figured holotype USNM 85587 from Fox River. Lea, 1874, Obs. Unio, 13: 55.

Unio ratus Lea 1872, Proc. Acad. Nat. Sci. Phila., 24: 160 (Neuse River, North Carolina). Lea, 1874, Jour. Acad. Nat. Sci. Phila., ser. 2, 8: 52, pl. 18, fig. 51; figured holotype USNM 85382. Lea, 1874, Obs. Unio, 13: 56.

Unio basalis Lea 1872, Proc. Acad. Nat. Sci. Phila., 24: 161 (Carter's Creek, near Columbus [Muscogee Co.], Georgia). Lea, 1874, Jour. Acad. Nat. Sci. Phila., ser. 2, 8: 48, pl. 16, fig. 46; figured holotype USNM 85703. Lea, 1874, Obs. Unio, 13: 52.

Unio dissimilis Lea 1872, Proc. Acad. Nat. Sci. Phila., 24: 161 (Long Creek, Gaston Co.; Pfeiffers Pond, [Charlotte], Mecklenburg Co.; *both* North Carolina). Lea, 1874, Jour. Acad. Nat. Sci. Phila., ser. 2, 8: 53, pl. 18, fig. 52; figured holotype USNM 86019 from Long Creek. Lea, 1874, Obs. Unio, 13: 57.

Unio cirratus Lea 1874, Proc. Acad. Nat. Sci. Phila. for 1873, 25: 422 (Abbeville District [Savannah River drainage], South Carolina). Lea, 1874, Jour. Acad. Nat. Sci. Phila., ser. 2, 8: 55, pl. 19, fig. 53; figured holotype USNM 85584. Lea, 1874, Obs. Unio, 13: 59.

Unio subolivaceus Lea 1874, Proc. Acad. Nat. Sci. Phila. for 1873, 25: 422 (Catawba River; Fox River [not located]; Yadkin River; *all* North Carolina). Lea, 1874, Jour. Acad. Nat. Sci. Phila., ser. 2, 8: 57, pl. 20, fig. 56; figured holotype USNM 85564. Lea, 1874, Obs. Unio, 13: 61.

Unio infulgens Lea 1874, Proc. Acad. Nat. Sci. Phila. for 1873, 25: 422 (Stewart's Pond, Union Co., North Carolina). Lea, 1874, Jour. Acad. Nat. Sci. Phila., ser. 2, 8: 60, pl. 21, fig. 59; figured holotype USNM 85403. Lea, 1874, Obs. Unio, 13: 64.

Unio corneus Lea 1874, Proc. Acad. Nat. Sci. Phila. for 1873, 25: 423 ([Chattahoochee River] Columbus [Muscogee Co.]; Marietta [Cobb Co.]; *both* Georgia. Abbeville District [Savannah River drainage], South Carolina). Lea, 1874, Jour. Acad. Nat. Sci. Phila., ser. 2, 8: 59, pl. 20, fig. 58; figured holotype USNM 85580. Lea, 1874, Obs. Unio, 13: 63.

Unio dooleyensis Lea 1874, Proc. Acad. Nat. Sci. Phila. for 1873, 25: 424 (Flint River, Dooley Co., Georgia; Abbeville District [Savannah River drainage] South Carolina). Lea, 1874, Jour. Acad. Nat. Sci. Phila., ser. 2, 8: 64, pl. 22, fig. 60; figured holotype USNM 85538 from Flint River. Lea, 1874, Obs. Unio, 13: 68.

Unio gesnerii Lea 1874, Proc. Acad. Nat. Sci. Phila. for 1873, 25: 424 (Uchee River [Russell Co., Alabama], near Columbus [Muscogee Co.], Georgia). Lea, 1874, Jour. Acad. Nat. Sci. Phila., ser. 2, 8: 65, pl. 22, fig. 64; figured holotype USNM 85670. Lea, 1874, Obs. Unio, 13: 69.

Unio invenustus Lea 1874, Proc. Acad. Nat. Sci. Phila. for 1873, 25: 424 ([Chattahoochee River] Columbus [Muscogee Co.]; Russell Co.; *both* Georgia. Irwin's Creek [Mecklenburg Co.], North Carolina). Lea, 1874, Jour. Acad. Nat. Sci. Phila., ser. 2, 8: 66, pl. 22, fig. 62; figured holotype USNM 85704 from Columbus, Georgia. Lea, 1874, Obs. Unio, 13: 70.

Unio (*Arconaia*) *provancheriana* Pilsbry 1890, Nat. Canadienne, 20: 171 (locality unknown). Pilsbry, 1891, Nautilus, 4: 127. Pilsbry, 1892, Proc. Acad. Nat. Sci. Phila., 44: 132, pl. 7, figs. 4–6; figured holotype ANSP 63094.

Unio palliatus 'Ravenel' Simpson 1900, Proc. United States Natl. Mus., 22: 730. [*nomen nudum*]. Listed under the synonymy of *Unio errans* Lea.

Unio pullatus majusculus De Gregorio 1914, Il Naturalista Siciliano, 22: 57, pl. 8, figs. a–d (Connecticut; type Palermo Museum, Sicily [not seen]).

Unio complanatus mainensis Rich 1915, Science, n. s., 42: 580 (Songo Pond about 3 miles South of Bethel [Oxford Co.], Maine; type, [location not known]).

Elliptio violaceus (Spengler). Ortmann, 1919, Mem. Carnegie Mus., 8: 94, pl. 8, figs. 4, 5.

Elliptio strigosus (Lea). *partim*. Clench and Turner, 1956, Bull. Florida State Mus., 1: 165.

Elliptio complanatus (Solander). Clarke and Berg, 1959, Cornell Univ. Exp. Sta. Mem. 367, p. 21, figs. 26–28. Athearn and Clarke, 1962, Natl. Mus. Canada, Bull., 183, p. 22, pl. 1, figs. 5, 6; pl. 4, figs. 7, 8.

Description. Shell large, often reaching over 100 mm in length. Outline generally long, trapezoidal, sometimes decidedly rhomboid, occasionally subelliptical. Valves generally flat or subinflated, though occasionally considerably inflated, thin to solid. Anterior end regularly rounded; posterior end usually broader and somewhat biangulate. Ventral margin straight or slightly arcuate, roughly parallel to the long straight or slightly curved dorsal margin, which forms an obtuse angle with the obliquely descending posterior margin. Hinge ligament prominent. Posterior ridge usually broad, double and rounded, sometimes rather angular, ending in a biangulation near the base. Posterior slope broad and unsculptured. Umbos low and uninflated, their sculpture consisting of strong ridges that run nearly parallel to the growth lines and are carried back to the nucleus behind as delicate radial lirae. Surface with irregular growth lines, often nearly smooth in young shells, becoming rougher in old ones. Periostracum brownish, or yellowish green, greenish brown, to almost black, often with green rays over the entire surface.

Left valve with two stumpy pseudocardinal teeth, one in front of the other, the more anterior one triangular, the hinder one generally not much elevated above the hinge line. Hinge line short and narrow; two long, straight, granular lateral teeth. Right valve with one chunky, serrated pseudocardinal, with a vestigial tooth in front of it; one lateral tooth. Beak cavities very shallow, with a few dorsal muscle scars. Anterior and posterior adductor muscle scars and pallial line all distinct. Nacre generally purplish, though often white, or slightly orange; iridescent, especially toward the margins.

Length mm	Height mm	Width mm	
154	82	44	Tar River, Bruce, 9 mi. NW Greenville, Pitt Co., North Carolina.
99	50	28	Savannah River, 7 mi. NE Newington, Screven Co., Georgia.
77	43	20	Turkey Creek, 4 mi. NE Allentown, Wilkinson Co., Georgia.

Anatomy. See Ortmann (1912a: 269). Discussed and figured by Reardon (1929: 11, pl. 4, figs. 1–10).

Breeding season. Ortmann (1919: 104) found gravid females from April 26 through July 16 during several years in Pennsylvania; the breeding season was restudied by Matteson (1948b: 704), who found that in the Ocqueoc River, lower Michigan, it extended from the middle of June to the middle of July.

Habitat. Found in lakes, ponds, small streams, and large rivers on nearly every type of substrate, though it appears to prefer sand. Throughout its range it is sometimes the only unionid found at some stations, and at others it is generally found in greater numbers than any other species save where its distribution overlaps *Elliptio icterina* (Conrad).

Remarks. Elliptio complanata (Lightfoot), which is found at scattered localities in the Apalachicola River system, is the most widely distributed and abundant unionid in the Atlantic Slope region, extending from the upper Altamaha River, Georgia, to northern Canada. It is a very variable species, but most nineteenth century authors agreed on uniting all of the ecophenotypes north of about the latitude of Washington under *complanata.* South of Washington, Isaac Lea, especially when in his seventies and eighties, applied specific names to the ecophenotypes of *complanata* and *icterina* as assiduously as Bourguignat and Locard did to the common European unionids, with the same confusion resulting. Simpson (1914, 2: 651) did a great deal to rectify the synonymy of *complanata.* This species, although variable in outline, degree of inflation, and color of both periostracum and nacre, is generally trapezoidal in outline, with the valves rather compressed, and when swollen, the greatest width is in the region of the posterior ridge. In large rivers such as the Savannah, Neuse, Tar, Roanoke, lower Potomac, and Connecticut, specimens reach maximum size, and tend to be subelliptical in outline with flattened valves, whereas in smaller rivers and tributaries they tend to be more rhomboid in outline and more inflated. Walter (1956: 266, 270) regarded the small creek form as *E. c. complanata* and called the large river form *E. complanata roanokensis* (Lea), even though both forms were found together at a number of the stations.

In the Altamaha River system *E. complanata* can be confused with *E. hopetonensis* (Lea) (under which see: *Remarks* on p. 325) which replaces it in the Altamaha River proper. It can also be confused with *E. icterina* (Conrad) (under which see: *Remarks* on p. 328) with whose several ecophenotypes it is often found, south of the White Oak River, North Carolina. In Georgia, *complanata* can not be confused with *Uniomerus tetralasmus* (Lea) with its acutely angled meeting of

the dorsal and posterior margins and its satiny periostracum. These characteristics become somewhat less constant in the Carolinas and northward, and *complanata* can be confused with it. However, *tetralasmus* tends to be more quadrate and to exhibit more swelling of the valves, and is always unrayed.

The specimens of *E. complanata* from Lake Creek, at Stone Mountain, De Kalb Co., Georgia, are among just a few records of Unionidae collected above the Fall Line in Georgia. Unfortunately, I misidentified them as *hopetonensis* for Raulerson and Burbank (1962, 9: 39).

Range. Apalachicolan region: restricted to the Apalachicola River system. Atlantic Slope region: Altamaha River system, Georgia, north to the St. Lawrence River system, Canada. Interior Basin: westward to Lake Superior, also parts of the Hudson Bay drainage. Discussed in detail and illustrated by Matteson (1948a: 13, fig. 2).

Specimens Examined

Altamaha River System

Oemulgee River Drainage. *Georgia*: Lake Creek at Stone Mountain, De Kalb Co. Walnut Creek, E Macon; Tobesofkee Creek, 5 mi. S Macon (USNM); *both* Bibb Co. Flat Creek, 2 mi. S Perry; Big Creek, 3 mi. S Henderson; *both* Houston Co. Buck Creek, 5 mi. NW Hawkinsville; Limestone Creek, 4.3 mi. E Hawkinsville; Cedar Creek, 5 mi. WSW Hawkinsville; Tuscawhatchee Creek, 5 mi. SW Hawkinsville; *all* Pulaski Co. Bluff Creek, 8 mi. NW Abbeville, Wilcox Co. Dicksons Creek, 10 mi. NW Fitzgerald, Ben Hill Co.

Oconee River Drainage. *Georgia*: Carters Creek, Baldwin Co. Turkey Creek, 4 mi. NE Allentown, Wilkinson Co. Ford Branch, 4 mi. W Dublin; Turkey Creek, 9 mi. W Dublin; *both* Laurens Co.

Ohoopee River Drainage. *Georgia*: Ohoopee River, 4 mi. S Wrightsville, Johnson Co.

Ogeechee River System

Ogeechee River Drainage. *Georgia*: Ogeechee River, Shoals, Warren Co. Ogeechee Creek, 4 mi. SW Mitchell, Glascock Co. Big Creek, 3 mi. SE Louisville; Williamson Swamp Creek, Bartow; Nails Creek, 2 mi. S Bartow; Rocky Creek, 2 mi. S Wadley; Big Creek, 3 mi. E Louisville; *all* Jefferson Co. Mill Creek, 5 mi. E Midville; Buckhead Creek, 14 mi. W Waynesboro; Buckhead Creek, 10 mi. SW Waynesboro; *all* Burke Co. Ogeechee River, Scarboro (MZUM); Ogeechee River, bridge, 1 mi. S Dover (MZUM); *both* Screven Co. Ogeechee River, bridge, 1 mi. E Blitchton (MZUM); Ogeechee River, Jinks Bridge, Route 16 (MZUM); Ogeechee River, Morgan Bridge, 14 mi. SE Pembroke (MZUM); *all* Bryan Co.

Savannah River System

Broad River Drainage. *Georgia*: Cadya Creek [not located] (MZUM). Broad River, 1.5 mi. S Bell; Broad River, Huguenot; *both* Elbert Co.

Savannah River Drainage. *South Carolina:* Abbeville Co. (USNM). Turkey Creek, 7 mi. NW Edgefield, Edgefield Co. *Georgia:* Savannah River, Augusta, Richmond Co. (MZUM). *South Carolina:* Lower Three Runs Creek, 8 mi. SW Barnwell, Barnwell Co.; Savannah River, 6 mi. W. Martin; Savannah River, Johnsons Landing, 10 mi. W Allendale; Savannah River, King Jaw Point, 10 mi. WSW Allendale (MZUM); *all* Allendale Co. *Georgia:* Brier Creek, Keysville (MZUM); Mill Race, 2 mi. N Sardis; *both* Burke Co. Savannah River, 7 mi. NE Newington, Screven Co. *South Carolina:* Mouth of Vermezobre Creek (Savannah River Wildlife Res.), Jasper Co. (MZUM). Savannah River, Savannah, Chatham Co.

Combahee River System

Salkehatchee River Drainage. *South Carolina:* Lemon Creek, 2.5 mi. S Bam-

berg; Little Salkehatchee River, 4 mi. N Ehrhardt; *both* Bamberg Co. Whippy Swamp Creek, 2.5 mi. NE Crocketville, Hampton Co.

Edisto River System

Edisto River Drainage. *South Carolina*: Snake Swamp Creek, Orangeburg Co., 6 mi. NE Bamberg, Bamberg Co. N. Fork Edisto River, Orangeburg, Orangeburg Co. Edisto River, Givhans Ferry, 2 mi. NW Givhans, Dorchester Co.

Ashley River System

Ashley River Drainage. *South Carolina*: [Ashley River] near Summersville, Dorchester Co.

Cooper-Santee River System

Saluda River Drainage. *South Carolina:* Saluda River, 2.3 mi. above Ware Shoals, Abbeville Co.

Broad River Drainage. *Tennessee*: Green River, 5 mi. ENE Mill Spring, Polk Co. *South Carolina:* Headwaters, Broad River, SE Reidsville, Spartenburg Co.

Congaree River Drainage. *South Carolina:* Congaree River, Columbia, Richland Co.

Catawba River Drainage. *North Carolina:* Catawba River, Bridgewater, Burke Co. Leppers Creek, Lincolnton, Lincoln Co. Mine Creek; Beaver Creek; *both* Gaston Co. Paw Creek; Stewarts Creek; Irwins Creek; Sugar Creek; Ashleys Creek; Long Creek; Catawba River; Bissels Pond, Charlotte; Pfeiffers Pond, Charlotte; Elias Pond, 10 mi. from Charlotte; *all* Mecklenburg Co. *South Carolina:* Branch, Little Dutchmans Creek, Rockhill, York Co.

Wateree River Drainage. *South Carolina*: Wateree River, 2.5 mi. W Camden, Kershaw Co.

Santee River Drainage. *South Carolina:* Poplar Creek, Schulers Fish Pond, near Santee State Park, Orangeburg Co., Wilsons Landing, 5 mi. NW Pineville; Santee Canal; *both* Berkeley Co.

Black River System

Black River Drainage. *South Carolina*: Sammy Swamp Creek, 6 mi. S Paxville, Clarendon Co.

Pedee River System

Lynches River Drainage. *South Carolina:* Lynches River, 2 mi. NE Bishopville, Lee Co.

Yadkin River Drainage. *North Carolina:* Yadkin River, Boomville, Yadkin Co. Yadkin River, Salisbury, Rowan Co. (MZUM). Ditch, Buffalo Creek, 6 mi. E Concord, Cabarrus Co. (MZUM). Uwharrie River, Montgomery Co. (USNM). Stewarts Pond, Union Co. (USNM).

Waccamaw River System

Waccamaw River Drainage. *North Carolina:* Lake Waccamaw, [town of] Lake Waccamaw, Columbus Co. *South Carolina:* Ditch, Waccamaw River, 1.25 mi. SE Conway, Horry Co. Waccamaw River, Wachasaw Landing, 2 mi. W Murrells Inlet, Georgetown Co.

Cape Fear River System

Deep River Drainage. *North Carolina*: Sandy Creek, Randolph Co. (MZUM). Rocky Run (USNM); Deep River, Gulf (Lea); *both* Chatham Co.

Cape Fear River Drainage. *North Carolina:* Haw River, 1.25 mi. NE Benaja, Rockingham Co. (MZUM). Buffalo Creek, 1 mi. E Greensboro, Guilford Co. (MZUM). Morgan Creek, 1 mi. SE Chapel Hill, Orange Co. (MZUM). New Hope River, Burke Forest, Durham Co. (MZUM). Rocky River, 11 mi. N Sanford, Chatham Co. Cape Fear River, Carlos; Cape Fear River, Kinnon; *both* Cumberland Co. (*both* MZUM). Ashe River, Pender Co. Greenfield Mill Pond, Wilmington, New Hanover Co. (USNM).

South River Drainage. *North Carolina*: Six Runs, Sampson Co. (USNM).

Neuse River System

Neuse River Drainage. *North Carolina*: North Flat River, 5.5 mi. S Roxboro Center,

Person Co. (81)[1] Eno River, 1.75 mi. ESE Hillsboro Center (117); S Fork, Little River, 0.5 mi. N Schley (104); Lake Michie, 12 mi. NNE Durham Center (75); Neuse River, 6 mi. ENE Durham Center (64); *all* Durham Co. Neuse River, 10.5 mi. NE Raleigh (49); Walnut Creek, 4.75 mi. WSW Raleigh (32); Swift Creek, 3 mi. WSW Garner (21); *all* Wake Co. Little River, 1.25 mi. NW Bagley (2); Neuse River, 3.5 mi. NNE Smithfield (26); *both* Johnston Co. Neuse River, Cliffs of Neuse State Park, 2 mi. NW Seven Springs, Wayne Co. Neuse River, 13.5 mi. WSW Kingston Center, Lenoir Co. Neuse River, Streets Ferry, 8.5 mi. NNW New Bern, Craven Co. Trent River, near Pollocksville, Jones Co. (MZUM).

Pamlico River System

Tar River Drainage. *North Carolina*: Tar River, Providence, Granville Co. Sandy Creek, Franklin Co. Stony Creek, Nashville, Nash Co. [Beach Swamp Creek] Enfield, Halifax Co. Swift Creek, Whitakers (MZUM); Tar River, Tarboro; Tar River, Old Sparta, 3.5 mi. W Pinetops; *all* Edgecomb Co. Tar River, Bruce, 9 mi. NW Greenville; Mill Run, Greenville; *both* Pitt Co.

Roanoke River System

Dan River Drainage. *Virginia*: Aarons Creek, 3 mi. W Buffalo Lithia Springs; Dan River; *both* Halifax Co. Bluestone Creek, near Clarksville, Mecklenburg Co.

Roanoke River Drainage. *Virginia*: Roanoke River, 4 mi. SW Elliston; N. Fork Roanoke River, Ironto (USNM); *both* Montgomery Co. Black Water River, Franklin Co. (MZUM). *North Carolina:* Roanoke River, Washington Co.

Chowan River System

Meherrin River Drainage. *Virginia*: Meherrin River, 2 mi. SW Grandy, Brunswick Co. Three Creek, near Emporia, Greensville Co. (MZUM). *North Carolina*: Meherrin River, Murfreesboro, Hertford Co. (USNM).

Nottoway River Drainage. *Virginia*: Tommeheton Lake, near Camp Pickett, Nottoway Co. Waqua Creek, 2 mi. SE Rawlings; Nottoway River, 3 mi. E Rawlings; *both* Brunswick Co.

Blackwater River Drainage. *Virginia*: Swift Creek, Rolling Mills, Chesterfield Co. Nansemond River, Nansemond Co.

Chowan River Drainage. *Virginia*: Chowan River, Edenhouse, 13 mi. E Windsor, Bertie Co.

James River System

James River Drainage. *Virginia*: Calfpasture River (Conrad, 1846: 407). North [= Maury] River, Lexington, Rockbridge Co. (USNM). Rivanna River, 2 mi. W Columbia, Fluvanna Co. James River, opposite Maidens, Goochland Co. James River, near Cartersville, Cumberland Co. James River, Richmond, Henrico Co. (MZUM).

Chickahominy River Drainage. *Virginia:* Chickahominy River, 4 mi. S Ashland, Hanover Co.

York River System

North Anna River Drainage. *Virginia*: Mine Run; Church River; *both* Orange Co., (*both* MZUM).

Rappahannock River System

Rapidan River Drainage. *Virginia*: Mountain Run, Orange Co. (USNM).

Rappahannock River Drainage. *Virginia:* Rappahannock River, 1 mi. S Remington, Faquier Co. Mountain Run, 3 mi. N

[1] Walter (1956) marked on a map of the Upper Neuse River some of the 136 stations he made during his survey in 1950–51. He collected *E. complanata* at forty of them. A selection of these with the station numbers included are presented here, since the localities have never been published. According to the author, most of the collections were made with a 1 8 inch mesh scraper net, which accounts for the paucity of specimens in most of the lots and also why this and other species were not found at more of the stations.

Lignum, Culpeper Co. Rappahannock River, Fredericksburg, Spotsylvania Co.

Occoquan Creek System

Occoquan Creek Drainage. *Virginia*: Bull Run, 3 mi. N Catharpin; Broad Run, [Fairfax Co.], 3 mi. W Manassas; Kettle Run, 1.5 mi. N Nokesville; *all* Prince William Co.

Potomac River System

Potomac River Drainage. *West Virginia:* Cacapon River, 1 mi. below Intermont, Hampshire Co. (USNM). Potomac River, Brosius, Morgan Co. Canal at Harpers Ferry, Jefferson Co. (MZUM). *Virginia:* [North River of S Fork Shenandoah River], Weyers Cave, Augusta Co. Passage Creek, 2 mi. SW Seven Fountains (USNM); N Fork Shenandoah River, E Woodstock; *both* Shenandoah Co. *Maryland*: Potomac River, 0.75 mi. W Point of Rocks, Frederick Co. *Virginia:* Potomac River, near Great Falls; Little Hunting Creek, near Mt. Vernon (MZUM); *both* Fairfax Co.

Elliptio (*Elliptio*) *hopetonensis* (Lea)

Plate 9: 1–2

Unio hopetonensis Lea 1838, Trans. Amer. Philos. Soc., 6: 29, pl. 9, fig. 24 ([Altamaha River] Hopeton, near Darien [McIntosh Co.], Georgia; figured holotype USNM 85391). Lea, 1838, Obs. Unio, 2: 29. Simpson, 1914, Cat. Naiades, 2: 668.

Unio inusitatis Lea 1859, Proc. Acad. Nat. Sci. Phila., 11: 171 (Swift Creek, below Macon [Bibb Co.], Georgia). Lea, 1860, Jour. Acad. Nat. Sci. Phila., ser. 2, 4: 333, pl. 52, fig. 158; figured holotype USNM 85531. Lea, 1860, Obs. Unio, 8: 15. Simpson, 1914, Cat. Naiades, 2: 670.

Description. Shell large, often exceeding 150 mm in length. Outline subrhomboid, narrower anteriorly. Valves rather flat to subinflated, occasionally quite inflated, the greatest inflation being about midway along the posterior ridge, they are thin to solid, inequilateral. Anterior end regularly rounded; posterior end broader, wedge-shaped or slightly biangulate. Ventral margin generally straight or slightly arcuate. Dorsal margin long and straight, tending to be a bit winglike where it joins the obliquely descending posterior margin in either a sharp or imperceptible angle. Hinge ligament prominent. Posterior ridge usually rather broad, single, and narrowly rounded above, becoming double below and ending in a wide biangulation at or above the posterior base. Posterior slope rather broad and unsculptured. Umbos low, slightly inflated, located in the anterior third of the shell, their sculpture consisting of several bars. Disk rather flat, or slightly concave when a slight umbonal-ventral sulcus is present. Periostracum brownish or yellowish green to olive green, often with green rays in young individuals, becoming rough and brownish or blackish in matures.

Left valve with two stumpy pseudocardinal teeth, one in front of the other, the more anterior one triangular, the hinder one generally not much elevated above the hinge line. Hinge line short and narrow, two long, straight, granular lateral teeth. Right valve with one chunky, serrated pseudocardinal, with a vestigial tooth in front of it; one lateral tooth. Beak cavities very shallow, with a few dorsal muscle scars. Anterior and posterior adductor muscle scars and pallial line all distinct. Nacre generally white or pinkish, occasionally purplish and iridescent, especially toward the margins.

Length mm	Height mm	Width mm	
150	75	38	Altamaha River, 3 mi. NW Everett City, Glynn Co., Georgia.
103	55	37	Ohoopee River, 3 mi. N Leman, Emanuel Co., Georgia.
84	43	20	Altamaha River, 4 mi. NE Jesup, Wayne Co., Georgia.

Anatomy. Discussed by Lea (1863: 415).

Habitat. Lives in sand or sandy mud in

the Altamaha River and its major tributaries.

Remarks. Elliptio hopetonensis (Lea), which is restricted to the Altamaha River system, is sympatric with *Elliptio complanata* (Lightfoot), which replaces *hopetonensis* in the smaller streams of the system. While *E. complanata* is very variable in both outline and degree of inflation, *E. hopetonensis* is quite constant in outline and in its lack of inflation. When somewhat inflated, as it is at the limits of its range, the greatest degree is near the mid portion of the posterior ridge. The posterior ridge is better defined in *hopetonensis* and the long dorsal margin tends to render most individuals wedge-shaped.

The large river form of *E. complanata* is admittedly very close to *hopetonensis*, but in river systems other than the Altamaha, where the large flat-sided form is found, more typical intergrades are generally present.

E. hopetonensis (Lea) has been confused with older specimens of *E. dariensis* (Lea), but the latter has a proportionally higher shell, with a sharper posterior ridge, often with sculpture on the posterior slope.

Range. Southern Atlantic Slope: restricted to the lower Altamaha River system, Georgia.

Specimens Examined

Altamaha River System

Ocmulgee River Drainage. *Georgia*: Swift Creek below Macon, Bibb Co. Ocmulgee River, Hawkinsville; Cedar Creek, Fountains Mill, 7 mi. SW Hawkinsville; *both* Pulaski Co. House Creek, Bowens Mill, 10 mi. N Fitzgerald, Ben Hill Co. Ocmulgee River, 1.5 mi. S Jacksonville, Telfair Co.

Little Ocmulgee River Drainage. *Georgia:* Gum Swamp Creek, 1 mi. N McRae, Telfair Co.

Oconee River Drainage. *Georgia*: Oconee River, 8 mi. SW Soperton, Treutlen Co. Oconee River, 2.5 mi. N Glenwood, Wheeler Co.

Ohoopee River Drainage. *Georgia*: Ohoopee River, Norristown; Ohoopee River, 3 mi. N Leman; *both* Emanuel Co. Ohoopee River, above Reidsville, Tattnall Co. (ANSP).

Altamaha River Drainage. *Georgia*: Altamaha River, 7 mi. N Hazlehurst, Jeff Davis Co. Altamaha River, 10 mi. N Baxley, Appling Co. Altamaha River, "Riverside Park," 4 mi. N Jesup, Wayne Co. Altamaha River, 3 mi. NE Everett City, Glynn Co. Altamaha River, near Fort Barrington; Altamaha River, Hopeton, near Darien; *both* McIntosh Co.

Elliptio (*Elliptio*) *icterina* (Conrad)

Plate 9: 3–10
Plate 10: 1–3

Unio icterinus Conrad, [May] 1834, New Fresh Water Shells United States, p. 41, pl. 6, fig. 5 (muddy shore, Savannah River, opposite Augusta [Richmond Co.], Georgia; figured holotype ANSP 41381). Published in May, *teste* Conrad, 1853, Proc. Acad. Nat. Sci. Phila., 6: 244, and not disputed by Lea, 1854, Proc. Acad. Nat. Sci. Phila., 7: 336–349. Conrad, 1836, Monography Unionidae, no. 4, p. 39, pl. 18, fig. 2.

Unio raveneli Conrad, [May] 1834, New Fresh Water Shells United States, p. 39, pl. 6, fig. 4 (Wateree Canal; since found in the small creeks near Cooper River; vicinity of Santee Canal; *all* South Carolina. Two syntypes ANSP 41370; the smaller one agrees with Conrad's description, but is not the figured specimen, which appears to be *Elliptio complanata* (Lightfoot). The second specimen is *Elliptio lanceolata* (Lea), *non Unio raveneliauus* Lea, 1834).

Unio watereensis Lea 1836, Synopsis Unionidae, p. 31. New name for *Unio raveneli* Conrad, 1834, *non Unio raveneliauus* Lea, 1834. As pointed out by Simpson, 1900, Proc. United States Natl. Mus., 22: 748, this change was unnecessary.

Unio confertus Lea, [August or September] 1834, Trans. Amer. Philos. Soc., 5: 103, pl. 16, fig. 47 (Santee Canal, South Carolina; type not in USNM [presumed lost]). Lea, 1834, Obs. Unio, 1: 215. Published in August or September 1834, *teste* Lea, 1854, Proc. Acad. Nat. Sci. Phila., 7: 244.

Unio lugubris Lea 1834, Trans. Amer. Philos.

Soc., 6: 30, pl. 9, fig. 25 ([Altamaha River], Hopeton, near Darien [McIntosh Co.], Georgia; figured holotype USNM 85638). Lea, 1838, Obs. Unio, 2: 30, *non* Say, 1832.

Unio geddingsianus Lea 1840, Proc. Amer. Philos. Soc., 1: 285 (Congaree River, South Carolina). Lea, 1842, Trans. Amer. Philos. Soc., 8: 202, pl. 11, fig. 15; figured holotype USNM 85650. Lea, 1842, Obs. Unio, 3: 40.

Unio fuscatus Lea 1843, Desc. Twelve Uniones (Black Creek, Florida). Lea, 1846, Trans. Amer. Philos. Soc., 9: 277, pl. 40, fig. 4; figured holotype USNM 85243. Lea, 1848, Obs. Unio, 4: 35.

Unio occultus Lea 1843, Desc. Twelve Uniones (Black Creek; Lake Monroe; *both* Florida). Lea, 1846, Trans. Amer. Philos. Soc., 9: 279, pl. 41, fig. 7; figured holotype USNM 85247, from Black Creek. Lea, 1848, Obs. Unio, 4: 37.

Unio limatulus Conrad 1849, Proc. Acad. Nat. Sci. Phila., 4: 154 (Savannah River, [Georgia]; type not in ANSP, [presumed lost]). Conrad, 1850, Jour. Acad. Nat. Sci. Phila., ser. 2, 1: 276, pl. 37, fig. 9. Conrad, 1853, Proc. Acad. Nat. Sci. Phila., 6: 251.

Unio tuomeyi Lea 1852, Trans. Amer. Philos. Soc., 10: 256, pl. 13, fig. 4 (Abbeville District [Savannah River drainage], South Carolina; figured holotype USNM 85669). Lea, 1852, Obs. Unio, 5: 12.

Unio whitcianus Lea 1852, Trans. Amer. Philos. Soc., 10: 258, pl. 14, fig. 8 (near Savannah [Chatham Co.], Georgia; figured holotype USNM 85658). Lea, 1852, Obs. Unio, 5: 14.

Unio barrattii Lea 1852, Trans. Amer. Philos. Soc., 10: 256, pl. 13, fig. 5 (Abbeville District [Savannah River drainage], South Carolina; figured holotype USNM 86010). Lea, 1852, Obs. Unio, 5: 12.

Unio pullatis Lea 1856, Proc. Acad. Nat. Sci. Phila., 8: 262 (creeks near Columbus [Muscogee Co.], Georgia). Changed to:

Unio pullatus Lea 1858, Jour. Acad. Nat. Sci. Phila., ser. 2, 4:57, pl. 8, fig. 39; figured holotype USNM 86020. Lea, 1858, Obs. Unio, 6: 57.

Unio coruscus Gould 1856, Proc. Boston Soc. Nat. Hist., 6: 15 (River Saint John's, near Lake Beresford, Florida; measured holotype MCZ 169097, figured by Frierson, 1911, Nautilus, 25, pl. 1, figs. 1–3, and by Johnson, 1964, United States Natl. Mus., Bull. no. 239, p. 60, pl. 32, fig. 3).

Unio micans Lea 1857, Proc. Acad. Nat. Sci. Phila., 9: 85 (Catawba River, Gaston Co.; Deep River, Gulf [Chatham Co.]; *both* North Carolina). Lea, 1862, Jour. Acad. Nat. Sci. Phila., ser. 2, 5: 59, pl. 3, fig. 207; figured holotype USNM 85077 from the Catawba River. Lea, 1862, Obs. Unio, 8: 63.

Unio obnubilus Lea 1857, Proc. Acad. Nat. Sci. Phila., 9: 169 (Buckhead Creek, Burke Co., Georgia). Lea, 1858, Jour. Acad. Nat. Sci. Phila., ser. 2, 4: 84, pl. 17, fig. 64; figured holotype USNM 85646. Lea, 1858, Obs. Unio, 6: 84.

Unio opacus Lea 1857, Proc. Acad. Nat. Sci. Phila., 9: 169 (Buckhead Creek, Burke Co., Georgia). Lea, 1858, Jour. Acad. Nat. Sci. Phila., ser. 2, 4: 86, pl. 18, fig. 66; figured holotype USNM 85546. Lea, 1858, Obs. Unio, 6: 86.

Unio similis Lea 1857, Proc. Acad. Nat. Sci. Phila., 9: 169 (Buckhead Creek, Burke Co., Georgia). Lea, 1858, Jour. Acad. Nat. Sci. Phila., ser. 2, 4: 91, pl. 19, fig. 71; figured holotype USNM 85653. Lea, 1858, Obs. Unio, 6: 91.

Unio sublatus Lea 1857, Proc. Acad. Nat. Sci. Phila., 9: 169 ([Chattahoochee River], Uchee Bar, below Columbus [Muscogee Co.], Georgia). Lea, 1858, Jour. Acad. Nat. Sci. Phila., ser. 2, 4: 82, pl. 16, fig. 62; figured holotype USNM 85897. Lea, 1858, Obs. Unio, 6: 82.

Unio viridicatus Lea 1857, Proc. Acad. Nat. Sci. Phila., 9: 170 (Buckhead Creek, Burke Co., Georgia). Lea, 1858, Jour. Acad. Nat. Sci. Phila., ser. 2, 4: 87, pl. 18, fig. 67; figured holotype USNM 85551. Lea, 1858, Obs. Unio, 6: 87.

Unio tetricus Lea 1857, Proc. Acad. Nat. Sci. Phila., 9: 170 (Flint River, near Albany [Dougherty Co.], Georgia). Lea, 1859, Jour. Acad. Nat. Sci. Phila., ser. 2, 4: 195, pl. 22, fig. 78; figured holotype USNM 85655. Lea, 1859, Obs. Unio, 7: 13.

Unio aequatus Lea 1857, Proc. Acad. Nat. Sci. Phila., 9: 170 (Buckhead Creek, Burke Co., Georgia). Lea, 1858, Jour. Acad. Nat. Sci. Phila., ser. 2, 4: 89, pl. 19, fig. 69; figured holotype USNM 85561. Lea, 1858, Obs. Unio, 6: 89.

Unio aquilus Lea 1857, Proc. Acad. Nat. Sci. Phila., 9: 172 (Flint River, Macon [County], Georgia). Lea, 1858, Jour. Acad. Nat. Sci. Phila., ser. 2, 4: 92, pl. 20, fig. 72; figured holotype USNM 85993. Lea, 1858, Obs. Unio, 6: 92.

Unio viridiradiatus Lea 1859, Proc. Acad. Nat. Sci. Phila., 11: 154 (Big Uchee River [Creek, Russell Co., Alabama] near Columbus, Georgia). Lea, 1860, Jour. Acad. Nat. Sci. Phila., ser. 2, 4: 336, pl. 53, fig. 161; figured holotype USNM 86018). Lea, 1860, Obs. Unio, 8: 18.

Unio hepaticus Lea 1859, Proc. Acad. Nat. Sci. Phila., 11: 154 (Salkehatchie River, South Carolina). Lea, 1860, Jour. Acad. Nat. Sci. Phila., ser. 2, 4: 348, pl. 57, fig. 173; figured holotype USNM 85559. Lea, 1860, Obs. Unio, 8: 30.

Unio viridans Lea 1859, Proc. Acad. Nat. Sci. Phila., 11: 170 (near Columbus [Muskogee Co.], Georgia). Lea, 1860, Jour. Acad. Nat. Sci. Phila., ser. 2, 4: 337, pl. 54, fig. 162; figured holotype USNM 85579. Lea, 1860, Obs. Unio, 8: 19.

Unio verutus Lea 1859, Proc. Acad. Nat. Sci. Phila., 11: 171 (Flat Rock Creek, near Columbus [Muscogee Co.], Georgia). Lea, 1860, Jour. Acad. Nat. Sci. Phila., ser. 2, 4: 335, pl. 53, fig. 160; figured holotype USNM 85899. Lea, 1860, Obs. Unio, 8: 17.

Unio ocmulgéensis Lea 1861, Proc. Acad. Nat. Sci. Phila., 13: 38 (Little Ocmulgee River, Lumber City [Telfair Co.], Georgia). Lea, 1862, Jour. Acad. Nat. Sci. Phila., ser. 2, 5: 95, pl. 14, fig. 243; figured holotype USNM 85901. Lea, 1862, Obs. Unio, 8: 99.

Unio merceri Lea 1862, Proc. Acad. Nat. Sci. Phila., 14: 169 (Lee Co., [Flint River drainage], Georgia). Lea, 1862, Jour. Acad. Nat. Sci. Phila., ser. 2, 5: 209, pl. 31, fig. 278, figured holotype USNM 86057. Lea, 1863, Obs. Unio, 9: 31.

Unio lucidus Lea 1863, Proc. Acad. Nat. Sci. Phila., 15: 192 (Livingston's Creek, Brunswick Co., [NE corner of Columbus Co., Cape Fear River drainage], North Carolina). Lea, 1866, Jour. Acad. Nat. Sci. Phila., ser. 2, 6: 9, pl. 2, fig. 6; figured holotype USNM 85242. Lea, 1867, Obs. Unio, 11: 13.

Unio livingstonensis Lea 1863, Proc. Acad. Nat. Sci. Phila., 15: 192 (Livingston's Creek, Brunswick Co., [NE corner of Columbus Co., Cape Fear River drainage] North Carolina). Lea, 1866, Jour. Acad. Nat. Sci. Phila, ser. 2, 6: 14, pl. 4, fig. 11; figured holotype USNM 85536. Lea, 1867, Obs. Unio, 11: 18.

Unio ablatus [*sic*] Lea 1863, Proc. Acad. Nat. Sci. Phila., 15: 193 (Long Creek, Gaston Co., North Carolina). Changed to:

Unio oblatus Lea 1866, Jour. Acad. Nat. Sci. Phila., ser. 2, 6: 13, pl. 4, fig. 10; figured holotype USNM 86001. Lea, 1867, Obs. Unio, 11: 17.

Unio radiolus Lea 1871, Proc. Acad. Nat. Sci. Phila., 23: 192 (Ogeechee River, Liberty Co., Georgia). Lea, 1874, Jour. Acad. Nat. Sci. Phila., ser. 2, 8: 21, pl. 6, fig. 18; figured holotype USNM 85621. Lea, 1874, Obs. Unio, 13: 25.

Unio cuspitatus Lea 1872, Proc. Acad. Nat. Sci. Phila., 24: 159 (Buckhead Creek, Burke Co., Georgia; Abbeville District [Savannah River drainage], South Carolina). Lea, 1874, Jour. Acad. Nat. Sci. Phila., ser. 2, 8: 43, pl. 14, fig. 50; figured holotype USNM 86014, from Buckhead Creek. Lea, 1874, Obs. Unio, 13: 47.

Unio hastatus Lea 1873, Proc. Acad. Nat. Sci. Phila., 25: 423 (New Market, Abbeville District [Savannah River drainage], South Carolina). Lea, 1874, Jour. Acad. Nat. Sci. Phila., ser. 2, 8: 56, pl. 19, fig. 54; figured holotype USNM 86013. Lea, 1874, Obs. Unio, 13: 60.

Unio fryanus B. H. Wright 1888, Proc. Acad. Nat. Sci. Phila., p. 113, pl. 2, fig. 1 (Lake Ashby, Volusia Co., Florida; figured holotype USNM 151032, refigured by Johnson, 1967, Occ. Papers on Moll., 3: 6, pl. 8, fig. 5).

Unio nolani B. H. Wright 1888, Proc. Acad. Nat. Sci. Phila., p. 116, pl. 4, fig. 11 (a creek flowing into St. Johns River, near Palatka [Putnam Co.], Florida; holotype USNM 151030, refigured by Johnson, 1967, Occ. Papers on Moll., 3: 7, pl. 10, fig. 4).

Unio simpsoni B. H. Wright 1888, Proc. Acad. Nat. Sci. Phila., p. 117, pl. 5, fig. 1 (Lake Woodruff, Volusia Co., Florida; holotype USNM 151038, refigured by Johnson, 1967, Occ. Papers on Moll., 3: 8, pl. 8, fig. 2).

Unio burtchianus S. H. Wright 1897, Nautilus, 10: 137 (St. Marys River, Nassau Co., Florida; lectotype USNM 149653, selected by Johnson, 1967, Occ. Papers on Moll., 3: 5, pl. 8, fig. 4, possibly the specimen figured by Simpson, 1900, Proc. Acad. Nat. Sci. Phila., p. 80, pl. 4, fig. 8).

Unio diazensis S. H. Wright 1897, Nautilus, 11: 5 (Lake Diaz, Volusia Co., Florida; lectotype USNM 149652, selected by Johnson, 1967, Occ. Papers on Moll., 3: 6, pl. 8, fig. 6).

Unio dispalans B. H. Wright 1899, Nautilus, 13: 50 (Suwannee River, Florida; holotype USNM 159986, figured by Simpson, 1900, Proc. Acad. Nat. Sci. Phila., p. 80, pl. 1, fig. 9, refigured by Johnson, 1967, Occ. Papers on Moll., 3: 6, pl. 8, fig. 3).

Unio singularis B. H. Wright 1899, Nautilus, 13: 75 (Spring Creek, [a branch of the Flint River], Decatur Co., Georgia; measured holotype USNM 159988, figured by Johnson, 1967, Occ. Papers on Moll., 3: 8, pl. 5, fig. 7).

Elliptio cylindraceus Frierson 1927, Check List North American Naiades, p. 29, new name for *Unio lugubris* Lea, 1838, *non* Say, 1832.

Elliptio maywebbae B. H. Wright 1934, Nautilus, 48: 28; *ibid.* 47, pl. 13, figs. 5–8 (near Seminole Springs [3.4 miles NE Sorrento], 15 miles SE of Eustis [Lake Co.], Florida, refigured by

Johnson, 1967, Occ. Papers on Moll., 3: 7, pl. 10, fig. 3).

Elliptio strigosus (Lea). *partim*. Clench and Turner, 1956, Bull. Florida State Mus., 1: 165.

Description. Shell generally small to medium, seldom reaching over 100 mm in length. Outline variable, subquadrate to subelliptical, sometimes rather pointed. Valves subinflated, subsolid to very solid, inequilateral. Anterior end regularly rounded; posterior end generally biangulate near the base, though sometimes rather produced and pointed. Ventral margin straight or slightly arcuate, sometimes obliquely descending. Dorsal margin slightly curved or almost straight, meeting the obliquely descending posterior margin in a more or less distinct angle. Hinge ligament long and low. Posterior ridge broadly rounded, generally faintly double. Posterior slope flat to slightly concave, sometimes with very faint radial sculpture present. Umbos broad and full but very low, located in the anterior quarter of the shell, their sculpture consisting of several double-looped ridges. Disk surface generally flat, or slightly concave when a slight umbonal-ventral sulcus is present. Periostracum generally fine and shiny, though sometimes heavy and rough, black, brownish black, or yellowish brown or bright yellow, chestnut, often with numerous very fine green rays.

Left valve with two stumpy pseudocardinal teeth, one in front of the other, often of about equal height. Hinge line short and narrow; two long straight lateral teeth. Right valve with two roughly parallel pseudocardinals, the posterior one apt to be serrated and chunky, the more anterior one low and vestigial; one lateral tooth. Beak cavities very shallow, with a few dorsal muscle scars. Anterior and posterior adductor muscle scars and pallial line all distinct. Nacre generally purplish, though sometimes salmon, bluish white, or pinkish, posteriorly iridescent.

Length mm	Height mm	Width mm	
98	49	29	Napiers Creek, 6 mi. N McIntyre, Wilkinson Co., Georgia.
81	42	28	Mill Race, 2 mi. N Sardis, Burke Co., Georgia.
88	50	30	Canoochee River, 2 mi. N Claxton, Evans Co., Georgia.

Habitat. Found in lakes, ponds, small streams, and large rivers, in nearly every type of substrate. *E. icterina* (Conrad) is sometimes found with *E. complanata* (Lightfoot) and other Unionidae at a given station, but like *complanata*, it is often found alone. In any case, one or the other of these species is generally more abundant than any other unionid at a given station.

Remarks. Elliptio icterina (Conrad), which ranges from the Escambia River system in the Apalachicolan region, east through northern Florida, and north to the White Oak River of North Carolina, is a very variable species and a number of populations have been named, some of them several times over. While some populations are more or less identifiable, there is usually a gradual transition of them between one river system and the next, such that while specimens from extremes of the range bear little resemblance to one another, there appears to be no point at which subspecies can be established. There is often a great deal of ecophenotypic variation, even at what appears to be a single station, the extremes usually connected by intergrades.

In the Apalachicolan region, *E. icterina* can be confused with *E. complanata* (Lightfoot) and *arctata* (Conrad). The latter is a rare species outside of the Alabama River system. It is distinctly and consistently arcuate with compressed valves, whereas *icterina* has a generally straight or curved ventral margin, is bluntly or acutely pointed posteriorly, and when occasionally produced post-basally, the valves are somewhat inflated. *Elliptio icterina*

occurs with *E. complanata* in the Apalachicola River system, and it can be distinguished from *complanata* by its less rhomboid, more elongate, often pointed shape.

The most common shape *E. icterina* takes in the Apalachicolan region is subrhomboidal to subelliptical, sometimes appearing quite pointed posteriorly if the biangulated posterior ridge ends near the medial line. The tendency to be pointed is more prevalent in specimens from the Apalachicolan region than in those from the Southern Atlantic Slope. The similarity of the populations of this species from the Chattahoochee River and the upper Savannah River, first noted in the localities of some of the taxa described by Isaac Lea, further confirms the commingling of the headwaters of these two systems. The shell form just described includes most of the taxa grouped by Simpson (1914, 2: 661) under *U. tuomeyi* Lea and by Clench and Turner (1956: 165–169) under *Elliptio strigosus* (Lea).

Noteworthy are the populations in Moccasin Creek of Econfina Creek, Bay Co., Florida, on the Gulf Coast: Black Creek, Florida, St. Marys and Canoochee rivers, Georgia, *all* on the Atlantic Slope; they resemble one another more than they do those from the several intervening river systems. The shells from these rivers tend to be more solid than those from elsewhere, to be more uniformly biangulate posteriorly, and to have a rather characteristic yellowish brown to shiny chestnut periostracum, often with fine dark green rays.

In northern Florida, there is an ecophenotype that lives in lakes and attains much less size than the river one. It has a heavy shell, but tends to be generally oval.

In the Wekiva River and Oklawaha rivers of the St. Johns River system, Florida, there occurs toward the headwaters of the streams and in springs a very thin, compressed, subrhomboidal ecophenotype that ends in a broad biangulation below the medial line, the shells of which tend to be heavier, more inflated, and produced postbasally. This shell form occurs again in abundance in Buckhead Creek of the Ogeechee River system; Brier Creek, of the Savannah River system; *both* Georgia; and the Salkehatchie River of South Carolina; *all* on the Atlantic Slope, which, similar to the Floridian rivers mentioned, are known to be rich in carbonates, Text-figure 4. That the shape of the shell is apparently environmentally controlled is also illustrated by the close resemblance of shells from Magnesia Springs, 3 miles W Hawthorn, Alachua Co., Florida; the headwaters of the Ogeechee River; and Cedar Spring, 2 mi. SE Bamberg, Bamberg Co., South Carolina. Though from widely separated drainage systems, shells from these stations bear a closer resemblance to one another than they do to specimens from other stations in their respective drainage systems. The shell form just described includes most of the taxa grouped by Simpson (1914, 2: 641) under *Unio obnubilis* Lea and some of those (1914, 2: 639) under *Unio confertus* Lea.

Especially on the Southern Atlantic Slope, often in the lower parts of rivers, specimens of *E. icterina* tend to be less subrhomboidal than elsewhere, but more elongate and inflated, with a tendency for the ventral margin to be slightly arcuate. The periostracum is often rough, black, and rayless. The shell form just described includes most of the taxa grouped by Simpson (1914, 2: 639) under *Unio confertus* Lea.

On the Atlantic Slope of Georgia, *E. icterina* (Conrad) is most easily confused with *Elliptio complanata* (Lightfoot) with which it is associated at many of the same stations, but *complanata* is quite consistently rhomboidal, and the valves are less inclined to be inflated. The periostracum of *icterina* is sometimes bright yellow or chestnut and is generally more shiny and smooth than that of *complanata*.

Range. Apalachicolan region: Escambia

River system, east to the St. Marys River system, Georgia. Peninsular Florida. Southern Atlantic Slope: Altamaha River system, Georgia, north to the White Oak River, North Carolina.

Specimens Examined

St. Marys River System

St. Marys River Drainage. *Georgia*: St. Marys River, 2 mi. E St. George; St. Marys River, Traders Hill; Spanish Creek, W Folkston; St. Marys River, 4 mi. SSE Folkston; *all* Charleton Co.

Altamaha River System

Ocmulgee River Drainage. *Georgia*: Swift Creek, near Macon; Tobesofkee Creek, 5 mi. S Macon; *both* Bibb Co. Mossy Creek, 2 mi. SW Kathleen, Houston Co. Limestone Creek, Brumbrys Mill, 4 mi. NE Hawkinsville; Cedar Creek, Fountains Mill, 7 mi. SW Hawkinsville; *both* Pulaski Co. House Creek, Bowens Mill, 9 mi. N Fitzgerald; Dicksons Creek, 10 mi. NE Fitzgerald; *both* Ben Hill Co.

Little Ocmulgee River Drainage. *Georgia:* Little Ocmulgee River, 6 mi. NE Cochran, Beckley Co. Alligator Creek, 2 mi. W Alamo, Wheeler Co. Gum Swamp Creek, 1 mi. N McRae; Little Ocmulgee River, Lumber City (USNM); *both* Telfair Co.

Oconee River Drainage. *Georgia*: Napiers Creek, 6 mi. N McIntyre, Wilkinson Co. Ford Branch, 4 mi. W Dublin; Turkey Creek, 9 mi. W Dublin, *both* Laurens Co.

Ohoopee River Drainage. *Georgia*: Ohoopee River, 4 mi. S Wrightsville; Ohoopee River, 2 mi. NE Adrian; *both* Johnson Co. Ohoopee River, 1 mi. E Adrian; Mulepen Creek, 2 mi. E Adrian; Ohoopee River, 1 mi. S Norristown; *all* Emanuel Co.

Little Ohoopee River Drainage. *Georgia:* Little Ohoopee River, 1 mi. E Kite, Johnson Co. Little Ohoopee River, 11 mi. W Swainsboro, Emanuel Co.

Altamaha River Drainage. *Georgia*: [Altamaha River], Hopeton near Darien, McIntosh Co. Frederica, Glynn Co.

Ogeechee River System

Canoochee River Drainage. *Georgia*: Canoochee River, Bulloch Co. Canoochee River, 2 mi. N Claxton, Evans Co. Canoochee River, near mouth, Bryan Co. (MZUM).

Ogeechee River Drainage. *Georgia*: Rocky Comfort Creek, 1 mi. N Louisville; Ogeechee River, 2 mi. S Louisville; Williamson Swamp Creek, Bartow; Nails Creek, 2 mi. S Bartow; *all* Jefferson Co. Barkeamp Creek, 7 mi. E Midville; Buckhead Creek, 14 mi. W Waynesboro; Buckhead Creek, 4 mi. E Vidotte; Buckhead Creek, 9 mi. SW Waynesboro; Mill Creek, 5 mi. NE Midville; Rocky Creek, 5 mi. SW Waynesboro; *all* Burke Co. Ogeechee River, Scarboro (MZUM); Chew Mill Creek, 8 mi. W Millen; Little Buckhead Creek, 1 mi. N Millen; *all* Jenkins Co.

Savannah River System

Savannah River Drainage. *South Carolina*: Abbeville District. (USNM). Turkey Creek, 7 mi. NW Edgefield, Edgefield Co. *Georgia*: Savannah River, 0.5 mi. S Augusta; Little Spirit Creek, DeBruce; *both* Richmond Co. *South Carolina:* Lower Three Runs Creek, 8 mi. SW Barnwell, Barnwell Co. Savannah River, 6 mi. W Martin; Savannah River, Johnsons Landing, 10 mi. W Allendale; *both* Allendale Co. *Georgia*: Savannah River, 7.5 mi. NE Shell Bluff; Newberry Creek, 2 mi. SE Shell Bluff; Beaverdam Creek, 7 mi. NW Girard; Sweetwater Creek, 2 mi. N Girard; *all* Burke Co. Brier Creek, 7.5 mi. NE Wrens, Jefferson Co. Brier Creek, Chalker Bridge, 6 mi. N Waynesboro, Burke Co. Brier Creek, 6 mi. N Sylvania, Screven Co. Rocky Creek, 6 mi. NW Sardis; Miami Branch, 3 mi. NW Sardis; Mill Race, 2 mi. N Sardis; *all* Burke Co. Near [city of] Savannah, Chatham Co. (USNM).

Combahee River System

Salkehatchee River Drainage. *South Carolina:* Salkehatchee River, Broxton Bridge; Whippy Swamp Creek, 2.5 mi. NE Crocketville; *both* Hampton Co.

Edisto River System

Edisto River Drainage. *South Carolina*: Snake Swamp Creek [Orangeburg Co.], 6 mi. NE Bamberg, Bamberg Co. N. Fork, Edisto River, Orangeburg, Orangeburg Co. Edisto River, Canadys Landing, 8 mi. SW St. George; Edisto River, Givhans Ferry, 2 mi. NW Givhans; *both* Dorchester Co.

Cooper-Santee River System

Broad River Drainage. *North Carolina*: Green River, 5 mi. ENE Mill Spring, Polk Co.

Catawba River Drainage. *North Carolina:* Catawba River, Bridgewater, Burke Co. Catawba River; Long Creek; Beaver Creek; *all* Gaston Co. Ashleys Creek; Bissels Pond, Charlotte; *both* Mecklenburg Co.

Wateree River Drainage. *North Carolina:* Wateree River, 2.5 mi. W Camden; Big Pine Tree Creek, 1.5 mi. S Camden; *both* Kershaw Co.

Santee River Drainage. *South Carolina*: Poplar Creek, Schulers Fish Pond, near Santee State Park, Orangeburg Co. Santee Canal; Cooper River (Conrad); near Charleston; *all* Berkeley Co.

Black River System

Black River Drainage. *South Carolina*: Cane Savannah Creek, 4 mi. SW Sumter; Pocotaligo Creek, 3 mi. S Sumter; [right branch] Pocotaligo River, 9 mi. SSE Sumter; Green Swamp Creek, 2.5 mi. W Sumter; *all* Sumter Co. Sammy Swamp Creek, 3 mi. S Paxville, Clarendon Co.

Pedee River System

Yadkin River Drainage. *North Carolina:* Yadkin River. Stewarts Pond, Union Co.

Pedee River Drainage. *South Carolina*: Lake Swamp Creek, 7.5 mi. ENE Oates, Darlington Co.

Waccamaw River System

Waccamaw River Drainage. *North Carolina:* Lake Waccamaw, [town of] Lake Waccamaw, Columbus Co. *South Carolina:* Ditch, Waccamaw River, 1.25 mi. SE Conway, Horry Co.

Cape Fear River System

Deep River Drainage. *North Carolina*: Deep River, Gulf (Lea), Chatham Co.

Cape Fear River Drainage. *North Carolina:* Rocky River, 11 mi. N Sanford, Chatham Co. Livingston Creek, Columbus Co. Ashe River, Pender Co. Cape Fear River.

White Oak River System

White Oak River Drainage. *North Carolina:* White Oak River, Maysville, Onslow Co.

Elliptio (Elliptio) arctata (Conrad)

Plate 10: 4–9

Unio arctatus Conrad 1834, Amer. Jour. Sci., 25: 340, pl. 1, fig. 9 (Black Warrior and Alabama Rivers [Alabama]; figured type not in ANSP. Lectotype, here selected, ANSP 41356, pl. 10, fig. 4, Alabama River, from T. A. Conrad). Conrad, 1834, New Fresh Water Shells United States, p. 36, pl. 5, fig. 4.

Unio strigosus Lea 1840, Proc. Amer. Philos. Soc., 1: 287 (Chattahoochee River, Columbus [Muscogee Co.], Georgia). Lea, 1842, Trans. Amer. Philos. Soc., 8: 198, pl. 9, fig. 9; figured holotype USNM 85890. Lea, 1842, Obs. Unio, 3: 36.

Unio tortivus Lea 1840, Proc. Amer. Philos. Soc., 1: 287 (Chattahoochee River, Columbus [Muscogee Co.], Georgia). Lea, 1842, Trans. Amer. Philos. Soc., 8: 204, pl. 12, fig. 17; USNM 85674 labeled type, does not agree exactly with the figure and is from Lee Co., Georgia, [Flint River drainage]. Lea, 1842, Obs. Unio, 3: 42.

Unio lazarus Lea 1852, Proc. Amer. Philos. Soc., 5: 251 (Abbeville District [Savannah River drainage], South Carolina). Lea, 1852, Trans. Amer. Philos. Soc., 11: 259, pl. 14, fig. 9; figured holotype USNM 86155. Lea, 1852, Obs. Unio, 5: 15.

Unio perstriatus Lea 1852, Proc. Amer. Philos. Soc., 5: 252 (Abbeville District [Savannah River drainage], South Carolina). Lea, 1852, Trans. Amer. Philos. Soc., 10: 255, pl. 12, fig. 3; figured holotype USNM 85892. Lea, 1852, Obs. Unio, 5: 11.

Unio gracilentus Lea 1857, Proc. Acad. Nat. Sci. Phila., 9: 85 (Catawba River, Gaston Co., North Carolina). Lea, 1862, Jour. Acad. Nat. Sci. Phila., ser. 2, 5: 58, pl. 3, fig. 205; figured holotype USNM 85976. Lea, 1862, Obs. Unio, 8: 62.

Unio perlatus Lea 1863, Proc. Acad. Nat. Sci. Phila., 15: 193 (Cape Fear River, Black Rock Landing [= 2 mi. S Kings Bluff, Bladen Co.], North Carolina). Lea, 1866, Jour. Acad. Nat. Sci. Phila., ser. 2, 6: 15, pl. 4, fig. 13; figured holotype USNM 86006. Lea, 1867, Obs. Unio, 11: 19.

Elliptio strigosus (Lea). *partim.* Clench and Turner, 1956, Bull. Florida State Mus., 1: 165.

Description. Shell small, seldom exceeding 60 mm in length. Outline elongated, subelliptical, distinctly arcuate. Valves compressed, subsolid, inequilateral. Anterior end regularly rounded; posterior end more broadly rounded, somewhat biangulate, produced and extending below the base line. Ventral margin arcuate. Dorsal margin slightly curved, usually indistinctly joining the obliquely descending posterior margin. Hinge ligament prominent, located near the middle of the shell. Posterior ridge low and rounded, usually with a faint second ridge above. Posterior slope slightly concave and smooth. Umbos not swollen, nor raised above the hinge line, located in the anterior sixth of the shell, their sculpture consisting of strong ridges. Disk generally slightly concave, caused by a slight umbonal-ventral sulcus. Surface with well-marked but delicate growth lines, often smooth and shiny, becoming darker and duller toward the borders. Periostracum usually greenish or yellowish with green rays over the entire surface becoming wider and more prominent posteriorly, sometimes dark burnt-brown especially on older shells.

Left valve with two low, rather vestigial, somewhat triangular pseudocardinal teeth. Hinge line short and very narrow; two low, short, straight lateral teeth. Right valve with one low but rather chunky pseudocardinal; one lateral tooth. Beak cavities very shallow, with a few dorsal muscle scars under the hinge plate. Anterior adductor muscle scars well impressed, posterior ones less so. Pallial line distinct, especially anteriorly. Nacre dirty white or purplish with yellowish splotches, slightly iridescent posteriorly.

Length mm	Height mm	Width mm	
55	22	14	Alabama River, Alabama. Lectotype of *Unio arctatus* Conrad.
56	24	13	Chattahoochee River, Columbus, Muscogee Co., Georgia. Holotype of *Unio strigosus* Lea.
52	23	12	Abbeville District, South Carolina. Holotype of *Unio lazarus* Lea.
49	25	15	Chattahoochee River, Columbus, Muscogee Co., Georgia. Figured type of *Unio tortivus* Lea, after Lea.

Habitat. Lives in rivers near the shore, among and under rocks.

Remarks. On the Atlantic Slope, *Elliptio arctata* (Conrad) is known only from the several type lots, and from a rather large unlocalized series from the Cape Fear River, North Carolina. In spite of the very erratic distributional pattern, there appears to be no morphological difference between the specimens from the Cape Fear River and those from the Alabama River system, where it is most abundant. It becomes distinctly rare eastward.

The thinness and compression of the valves, subelliptical outline, somewhat produced posterior end, and quite consistently arcuate ventral margin distinguish this species from any other *Elliptio* in the Atlantic Slope region.

Range. Alabama-Coosa River system. Apalachicolan region: Escambia River system, east to the Apalachicola River system, but discontinuous. Southern At-

lantic Slope: upper Savannah River system, South Carolina; Catawba River, North Carolina of the Cooper-Santee River system, Lower Cape Fear River system, North Carolina.

Specimens Examined

Savannah River System

Savannah River Drainage. *South Carolina:* Abbeville District (USNM).

Cooper-Santee River System

Catawba River Drainage. *North Carolina:* Catawba River, Gaston Co. (USNM).

Cape Fear River System

Cape Fear River Drainage. *North Carolina:* Cape Fear River, Black Rock Landing, 2 mi. S Kings Bluff, Bladen Co. (USNM). Cape Fear River.

Elliptio (Elliptio) lanceolata (Lea)

Plate 10: 10
Plate 11: 1–6

Obliquaria cuprea Rafinesque 1820, Ann. Gén. Sci. Phys. (Bruxelles), 5: 304, pl. 81, figs. 8, 9 (Le Monongahela et le Potowmak; type not in ANSP [lost]). Ortmann and Walker (1922: 31) have pointed out that this species might be either *E. dilatata* Rafinesque, of the Monongahela River or *producta* Conrad [= *lanceolata* Lea] of the Potomac River. Conrad (1834: 68), as first reviser of this species, referred it to *dilatata*. The type locality is here restricted to the Monongahela River, Pennsylvania, and *O. cuprea* remains a synonym of *E. dilatata* Rafinesque.

Unio lanceolatus Lea 1828, Trans. Amer. Philos. Soc., 3: 266, pl. 3, fig. 2 (Tar River, Tarborough [Edgecombe Co.], North Carolina; figured holotype USNM 85905). Lea, 1834, Obs. Unio, 1: 8.

Unio angustatus Lea 1831, Trans. Amer. Philos. Soc., 4: 114, pl. 17, fig. 43 (Cooper River, South Carolina; figured holotype USNM 85896; Congaree River, South Carolina). Lea, 1834, Obs. Unio, 1: 124.

Unio productus Conrad 1836, Monography Unionidae, no. 3, p. 31, pl. 14, fig. 1 (Savannah River, Augusta [Richmond Co., Georgia]; figured holotype ANSP 41397).

Unio fisherianus Lea 1838, Trans. Amer. Philos. Soc., 6: 8, pl. 4, fig. 8 (Head of Chester River [Kent Co.], Maryland; figured holotype USNM 86022). Lea, 1838, Obs. Unio, 2: 8.

Unio foliculatus Lea 1838, Trans. Amer. Philos. Soc., 6: 38, pl. 11, fig. 33 (Savannah River, [Georgia]; figured holotype USNM 85861). Lea, 1838, Obs. Unio, 2: 38.

Unio duttonianus Lea 1841, Proc. Amer. Philos. Soc., 2: 31 (Ogeechee Canal, Savannah [Chatham Co.], Georgia). Lea, 1842, Trans. Amer. Philos. Soc., 8: 236, pl. 22, fig. 50; type not in USNM [lost]. Lea, 1842, Obs. Unio, 3: 74.

Unio sagittiformis Lea 1852, Trans. Amer. Philos. Soc., 10: 277, pl. 22, fig. 35 (Oconee River, near Athens [Clarke Co.], Georgia; figured holotype USNM 85970). Lea, 1852, Obs. Unio, 5: 33.

Unio rostraeformis Lea 1856, Proc. Acad. Nat. Sci. Phila., 8: 262 (Swift Creek, near Macon [Bibb Co.], Georgia). Changed to:

Unio rostriformis Lea 1858, Jour. Acad. Nat. Sci. Phila., ser. 2, 4: 64, pl. 10, fig. 46; probable figured holotype USNM 85973. Lea, 1858, Obs. Unio, 6: 64.

Unio extensus Lea 1857, Proc. Acad. Nat. Sci. Phila., 9: 31 (Dry Creek, near Columbus [Muscogee Co.], Georgia). Lea, 1858, Jour. Acad. Nat. Sci. Phila., ser. 2, 4: 68, pl. 12, fig. 49; figured holotype USNM 85995. Lea, 1858, Obs. Unio, 6: 67.

Unio emmonsii Lea 1857, Proc. Acad. Nat. Sci. Phila., 9: 86 (Roanoke River, Weldon [Halifax Co.], North Carolina). Lea, 1862, Jour. Acad. Nat. Sci. Phila., ser. 2, 5: 56, pl. 2, fig. 203; figured holotype USNM 86028. Lea, 1862, Obs. Unio, 8: 60.

Unio naviculoides Lea 1857, Proc. Acad. Nat. Sci. Phila., 9: 170 (Buckhead Creek, Burke Co.; Macon [Bibb Co.]; *both* Georgia). Lea, 1858, Jour. Acad. Nat. Sci. Phila., ser. 2, 4: 94, pl. 20, fig. 74; figured holotype USNM 86005, from Buckhead Creek, Lea, 1858, Obs. Unio, 6: 94.

Unio maconensis Lea 1857, Proc. Acad. Nat. Sci. Phila., 9: 172 (Flint River, near Macon [Co.], Georgia). Lea, 1858, Jour. Acad. Nat. Sci. Phila., ser. 2, 4: 93, pl. 20, fig. 73; figured holotype USNM 86004. Lea, 1858, Obs. Unio, 6: 93.

Unio hazelhurstianus Lea 1858, Proc. Acad. Nat. Sci. Phila., 9: 166 (Satilla River, Camden Co., Georgia). Lea, 1859, Jour. Acad. Nat. Sci. Phila., ser. 2, 4: 211, pl. 26, fig. 92; figured holotype USNM 86009. Lea, 1859, Obs. Unio, 7: 29.

Unio viridulus Lea 1863, Proc. Acad. Nat. Sci. Phila., 15: 193 (Neuse River, near [6 miles E of] Raleigh [Wake Co.], North Carolina). Lea, 1866, Jour. Acad. Nat. Sci. Phila., ser. 2, 6:

10, pl. 3, fig. 7; figured holotype USNM 85908. Lea, 1867, Obs. Unio, 11: 14.

Unio nasutilus Lea 1863, Proc. Acad. Nat. Sci. Phila., 15: 192 (Livingston's Creek, Brunswick Co. [NE corner of Columbus Co., Cape Fear River drainage], North Carolina). Changed to:

Unio nasutulus Lea 1866, Jour. Acad. Nat. Sci. Phila., ser. 2, 6: 12, pl. 3, fig. 9; figured holotype USNM 86027. Lea, 1867, Obs. Unio, 11: 16.

Unio attenuatus Lea 1872, Proc. Acad. Nat. Sci. Phila., 24: 157 (Savannah River; Beaver Creek [few miles E of Bonaire, Ocmulgee River drainage], Houston Co.; *both* Georgia). Lea, 1874, Jour. Acad. Nat. Sci. Phila., ser. 2, 8: 41, pl. 14, fig. 38; figured holotype USNM 85974, from Beaver Creek. Lea, 1874, Obs. Unio, 13: 45.

Unio rostellum Lea 1872, Proc. Acad. Nat. Sci. Phila., 24: 160 (Macon [Bibb Co.], Georgia). Lea, 1874, Jour. Acad. Nat. Sci. Phila., ser. 2, 8: 44, pl. 15, fig. 41; figured holotype USNM 85972. Lea, 1874, Obs. Unio, 13: 48.

Unio exactus Lea 1872, Proc. Acad. Nat. Sci. Phila., 24: 159 (Savannah River at Governor Hamilton's [Mansion, 8 mi. S of Hardeeville, Jasper Co., South Carolina], Georgia). Lea, 1874, Jour. Acad. Nat. Sci. Phila., ser. 2, 8: 45, pl. 15, fig. 43; figured holotype USNM 85872. Lea, 1874, Obs. Unio, 13: 49.

Unio subcylindraceus Lea 1873, Proc. Acad. Nat. Sci. Phila., 25: 422 (Rocky Creek, near Macon [Bibb Co.]; Carter's Creek [Baldwin Co.]; *both* Georgia). Lea, 1874, Jour. Acad. Nat. Sci. Phila., ser. 2, 8: 58, pl. 20, fig. 57; figured holotype USNM 85863, from Rocky Creek. Lea, 1874, Obs. Unio, 13: 62.

Unio arctior fisheropsis De Gregorio 1914, Il Naturalista Siciliano, 22: 45, pl. 5, figs. 3a-c (Ogeecho [Ogeechee] Canal [Chatham Co.], Georgia; type Palermo Mus., Sicily [not seen]).

Elliptio cupreus (Rafinesque). Ortmann, 1919, Mem. Carnegie Mus., 8: 110, pl. 8, fig. 6.

Elliptio fisherianus (Lea). Ortmann, 1919, Mem. Carnegie Mus., 8: 113, pl. 8, fig. 7.

Description. Shell generally medium throughout most of its range, usually not exceeding 100 mm in length, though reaching over 130 mm in a few localities. Outline elongated trapezoid, or elongated ovate, lance-head shaped, a little over twice as long as high. Valves usually subcompressed, thin to subsolid, occasionally quite solid; inequilateral. Anterior end regularly rounded; posterior end elongated and either sharply or bluntly pointed. The posterior point may occasionally be sharp and turned up above the medial line; sometimes it drops below the medial line, but more generally it is evenly and broadly pointed. Ventral margin gently curved, sometimes almost straight, or a bit arcuate. Dorsal margin straight, forming an indistinct angle with the obliquely descending posterior slope. Hinge ligament rather long and low. Posterior ridge rather broadly rounded or subangular, generally with a secondary ridge above it; the ridges sometimes cause the point to be slightly biangulate. Umbos very low, located in the anterior fourth of the shell, their sculpture consisting of several corrugated, longitudinal ridges. Disk rather flat, or just slightly concave caused by a slight umbonal-ventral sulcus. Surface of the shell with numerous concentric striae. Periostracum fine, subshiny, greenish yellow, olive, often with distinct greenish rays, especially when young, but often becoming rough and brownish or dirty black with age.

Left valve with two stumpy pseudocardinal teeth, one in front of the other, both somewhat triangular; the hinder one may be vestigial. Hinge line rather short and narrow; two long, straight lateral teeth. Right valve with two roughly parallel pseudocardinals, the posterior one inclined to be triangular, serrated and chunky, the more anterior one, low and vestigial; one lateral tooth. Beak cavities very shallow, with a few dorsal muscle scars. Anterior and posterior adductor muscle scars and pallial line all distinct. Nacre white, bluish white, pinkish, purplish, posteriorly iridescent.

Length mm	Height mm	Width mm	
134	54	29	Ochee Creek, about 5 mi. SE Toomsboro, Wilkinson Co., Georgia.
99	42	20	Mill Race, 2 mi. N Sardis, Burke Co., Georgia.
74	28	14	As above.
68	22	12	As above.

Anatomy. Discussed and figured by Reardon (1929: 11, pl. 5, figs. 1–10). The glochidia are hookless.

Breeding season. Ortmann (1919: 111) found gravid females on May 6, June 3–8, 1912, in the Potomac and James Rivers, Virginia.

Habitat. Lives on sandy bottoms, often found crawling about with much of the shell out of the sand, also found among rocks and in mud, where the current is not too swift.

Remarks. Elliptio lanceolata (Lea), which ranges from the Escambia River system of Florida to the Juniata River of the Susquehanna River system of Pennsylvania, is allied to *Elliptio icterina* (Conrad) and *complanata* (Lightfoot) of the Apalachicolan and Atlantic Slope regions. While *complanata* has a subtrapezoidal shape, *lanceolata* is generally easily distinguished from it by its more elongate, lanceolate shape. Even though the posterior point may be somewhat rounded, it can usually be separated from *complanata* or *icterina* because it is over twice as long as high and because the dorsal and ventral margins are roughly parallel.

On the Atlantic Slope, *E. lanceolata* is most easily confused with *Ligumia nasuta* (Say), which ranges from the James River, Virginia, to the St. Lawrence River, Canada. Anatomically they are quite different, and the shells of *nasuta* show sexual dimorphism and a pattern of green rays that is not found in *lanceolata*. The male shells can be confused, but *nasuta* has a silvery white or cream colored nacre, whereas *lanceolata* may be coppery or purple, with more stumpy hinge teeth. The females of *nasuta* have a peculiar expansion of the lower margin, rendering them easy to distinguish.

Ortmann (1919: 113) separated *fisherianus* from *lanceolata* with some reluctance, on the basis that *fisherianus* was slightly more elongated, with a greater taper to the posterior part of the shell. A few populations of this ecophenotype are found in the northern range of the species and again in the ponds near Wilmington, New Hanover Co., North Carolina.

Reardon (1929: 9) notes that there is no constant distinction either in the anatomy or in the shell morphology. Except for their large size, specimens from Ochee Creek, about 5 mi. SE Toomsboro, Wilkinson Co., Georgia, show the same range of variation as do specimens from the Potomac River, Virginia.

There is much local variation in this species throughout its range, and it is easy to see how Issac Lea fell to naming all of the shell forms. The specimens from the type locality and from several other of the rivers in North Carolina are usually small, shiny, and yellowish, without a trace of rays, whereas over the rest of its range, *lanceolata* generally has greenish rays. The species varies considerably as to the ratio of height to length, the sharpness of the posterior point, whether the point is above or below the medial line, and even to the degree of inflation. It can generally be easily separated from any other species of *Elliptio* because it is more than twice as long as high, with the dorsal and ventral margins roughly parallel.

Also found on the Southern Atlantic Slope is *Elliptio shepardiana* (Lea), which is restricted to the Altamaha River system, Georgia, and although it is obviously closely related to *lanceolata*, it differs from *lanceolata* by being over three times as long as high.

In the Suwannee River system of the Apalachicolan region and in Peninsular Florida, *E. lanceolata* is replaced by a closely related species, *Elliptio jayensis* (Lea). While *jayensis* exhibits a range of variation similar to that of *lanceolata*, it is generally smaller, with a tendency to be higher behind. The dorsal and ventral margins are not parallel, and it has more numerous darker green rays.

In the Apalachicolan region, it is often difficult to separate *lanceolata* from *Elliptio icterina* (Conrad), which also some-

times tends to have a lanceolate shell, but even so, these strikingly long shells can generally be separated from any other *Elliptio* by their height to length ratio.

Elliptio lanceolata (Lea) seems to be most abundant on the Atlantic Slope of Georgia. Here and in the Apalachicolan region, individuals reach their greatest size. Specimens from the Carolinas and the north are generally smaller and more delicate.

Range. Apalachicolan region: Escambia River system, east to the Apalachicola River system, but discontinuous; Satilla River system, Georgia. Atlantic Slope: Altamaha River system, Georgia, north to the Juniata River of the Susquehanna River system, Pennsylvania.

Specimens Examined

Satilla River System

Satilla River Drainage. *Georgia*: Satilla River, Camden Co.

Altamaha River System

Ocmulgee River Drainage. *Georgia*: Walnut Creek, 2 mi. E Macon; Rocky Creek (USNM); Swift Creek, 4 mi. E Macon; Tobesofkee Creek, 5 mi. S Macon; *all* Bibb Co. Beaver Creek, E Bonaire (USNM); Mossy Creek, 2 mi. SW Kathleen; Flat Creek, 2 mi. S Perry; *all* Houston Co. Buck Creek, 5 mi. NW Hawkinsville; Limestone Creek, 4.3 mi. E Hawkinsville; Big Tuscawhatchee Creek, 5 mi. SW Hawkinsville; Cedar Creek, Fountains Mill, 7 mi. SW Hawkinsville; Mosquito Creek, 8 mi. SE Hawkinsville; *all* Pulaski Co. House Creek, Bowens Mill, 9 mi. N Fitzgerald; Dicksons Creek, 10 mi. NE Fitzgerald; *both* Ben Hill Co.

Little Ocmulgee River Drainage. *Georgia:* Little Ocmulgee River, 7 mi. NE Cochran, Beckley Co. Gum Swamp Creek, 1 mi. N McRae, Telfair Co.

Oconee River Drainage. *Georgia*: Oconee River, near Athens, Clarke Co. (USNM). Carters Creek, Baldwin Co. (USNM). Napiers Creek, 6 mi. N McIntyre; Ochee Creek, about 5 mi. SE Toomsboro; Turkey Creek, 4 mi. NE Allentown; *all* Wilkinson Co. Ford Branch, 4 mi. W Dublin; Turkey Creek, 9 mi. W Dublin; Rocky Creek, 8 mi. W Dudley; *all* Laurens Co. Ochwalkee Creek, 2 mi. E Glenwood, Wheeler Co.

Ohoopee River Drainage. *Georgia*: Ohoopee River, 4 mi. S Wrightsville, Johnson Co. Mulepen Creek, 2 mi. E Adrian; Ohoopee River, Norristown; *both* Emanuel Co.

Little Ohoopee River Drainage. *Georgia:* Battleground Creek, 1 mi. N Kite, Johnson Co.

Ogeechee River System

Ogeechee River Drainage. *Georgia*: [Williamson Swamp Creek] Bartow; Nails Creek, 2 mi. S Bartow; *both* Jefferson Co. Bark Camp Creek, 7 mi. E Midville; Mill Creek, 5 mi. E Midville; Buckhead Creek, 9 mi. S Waynesboro; *all* Burke Co. Ogeechee River, bridge 1.5 mi. SW Oliver, Screven Co. (MZUM). Ogeechee River, bridge, 1 mi. E Blitchton; Ogeechee River, Jinks Bridge [Rte. 16]; Dolly Lake, about 1.5 mi. below Kiterlighter Camp; *all* Bryan Co. (*all* MZUM).

Savannah River System

Savannah River Drainage. *Georgia*: Savannah River, Augusta, Richmond Co. (ANSP). Brier Creek, 7.5 mi. NE Wrens, Jefferson Co. Savannah River, 7.5 mi. NE Shell Bluff; Brier Creek, Chalker Bridge, 6 mi. N Waynesboro; Mill Race, 2 mi. N Sardis; *all* Burke Co. *South Carolina*: Savannah River, 2 mi. SW Millettville (MZUM); Savannah River, Johnsons Landing, 10 mi. W Allendale; *both* Allendale Co. *Georgia:* Savannah River, 8 mi. S Hardeville, Jasper Co. (USNM). Rice fields, near Savannah; Ogeechee Canal, Savannah (Lea); *both* Chatham Co.

Edisto River System

Edisto River Drainage. *South Carolina*: Edisto River [not localized].

Cooper-Santee River System

Cooper River Drainage. *South Carolina:* Cooper River [not localized].

Saluda River Drainage. *South Carolina:* Saluda River, 2.3 mi. above Ware Shoals, Abbeville Co.

Congaree River Drainage. *South Carolina:* Congaree River, Richland Co.

Wateree River Drainage. *South Carolina:* Wateree River, 2.5 mi. W Camden, Kershaw Co.

Black River System

Black River Drainage. *South Carolina*: Green Swamp Creek, 2.5 mi. W Sumter; Pocotaligo River, 3 mi. S Sumter; *both* Sumter Co.

Waccamaw River System

Waccamaw River Drainage. *South Carolina*: Lake Waccamaw, [town of] Lake Waccamaw, Columbus Co.

Cape Fear River System

Cape Fear River Drainage. *North Carolina:* Livingstons Creek, Brunswick Co. (USNM). Wilmington, New Hanover Co.

Neuse River System

Neuse River Drainage. *North Carolina*: Little River, Tarpleys Mill, 2 mi. NE Wendell (5); Little River, 2 mi. WSW Zebulon (6); *both* Wake Co. Neuse River, 6 mi. E Raleigh (USNM).

Pamlico River System

Tar River Drainage. *North Carolina*: Tar River, Tarboro (USNM); Tar River, Old Sparta, 3.5 mi. W Pinetops; *both* Edgecombe Co.

Roanoke River System

Dan River Drainage. *Virginia*: Dan River [Halifax Co.].

Roanoke River Drainage. *Virginia*: Roanoke River, Weldon, Halifax Co.

Chowan River System

Nottoway River Drainage. *Virginia*: Nottoway River, 3 mi. E Rawlings, Brunswick Co.

James River System

James River Drainage. *Virginia*: Calfpasture River (Conrad, 1846: 407); North [= Maury] River, Lexington; [James River], near Natural Bridge; *all* Rockbridge Co. James River, Buchanan, Botetourt Co. James River, Lynchburg, Campbell Co. Rivanna River, 2 mi. W Columbia, Fluvanna Co. James River, opposite Maidens, Goochland Co.

York River System

South Anna River Drainage. *Virginia*: South Anna River, 1 mi. N. Dabneys, Louisa Co. South Anna River, Gum Tree, Hanover Co.

Rappahannock River System

Rapidan River Drainage. *Virginia*: Rapidan River, N Unionville, Orange Co. Branch, N Lignum, Culpeper Co.

Rappahannock River Drainage. *Virginia:* Rappahannock River, Remington, Faquier Co. Rappahannock River, Waterloo, Culpeper Co.

Occoquan Creek System

Occoquan Creek Drainage. *Virginia*: Broad Run [Fairfax Co.] 3 mi. W Manassas, Prince William Co.

Potomac River System

Potomac River Drainage. *West Virginia*: Back Creek, 0.5 mi. E Glengary, Berkeley Co. Shenandoah River, Jefferson Co. *Virginia*: N Fork Shenandoah River, E Woodstock, Shenandoah Co. *Pennsylvania*: Rock Creek, 0.75 mi. N Gettysburg, Adams Co. *Maryland*: Aqueduct Lake Washington Co. Flat Run, Emmitsburg; Monocacy River, 2 mi. W Pleasant; *both* Frederick Co. Potomac River, Great Falls;

Potomac River, below Alexandria; *both* Fairfax Co.

Elliptio (Elliptio) shepardiana (Lea)

Plate 11: 7

Unio shepardianus Lea 1834, Trans. Amer. Philos. Soc., 5: 95, pl. 13, fig. 38 [Altamaha River] Hopeton, near Darien [McIntosh Co.], Georgia; type, not in USNM [lost]; three presumed paratypes MCZ 155568 ex Prof. Shepard. Lea, 1834, Obs. Unio, 1: 207. Simpson, 1914, Cat. Naiades, 2: 698.

Description. Shell often large, reaching over 185 mm in length. Outline extremely elongate, trapezoidal, lance-head shaped, over three times as long as high. Valves subcompressed to subinflated, subsolid, quite inequilateral. Anterior end regularly rounded, usually higher than any other part of the shell; posterior end very elongated and pointed. The point may be at the medial line or below it. Ventral margin almost always arcuate. Dorsal margin roughly parallel to the ventral margin, long and straight, forming an indistinct angle with the obliquely descending posterior margin. Hinge ligament long and low. Posterior ridge rather broadly rounded or subangular, generally with a secondary ridge above it; the ridges sometimes cause the point to be slightly biangulate. Umbos very low, located in the anterior fifth of the shell, their sculpture consisting of several corrugated, longitudinal ridges. Disk surface flat or just slightly concave caused by a slight umbonal-ventral sulcus. Surface of the shell with numerous concentric striae. Periostracum fine, greenish or yellowish, with faint rays when young, becoming rough and brownish or blackish with age.

Left valve with two stumpy pseudocardinal teeth, one in front of the other, both somewhat triangular, the hinder one less high. Hinge line rather short and narrow; two long straight lateral teeth. Right valve with two roughly parallel pseudocardinals, the posterior one inclined to be triangular, serrated, and chunky, the more anterior one low and vestigial; one lateral tooth. Beak cavities very shallow, with a few dorsal muscle scars. Anterior and posterior adductor muscle scars and pallial line all distinct. Nacre sometimes bluish white or pinkish but usually purplish or coppery, iridescent posteriorly.

Length mm	Height mm	Width mm	
185	42	26	Altamaha River, 3 mi. NW Everett City, Glynn Co., Georgia.
127	29	15	Ocmulgee River, 1 mi. S Lumber City, Telfair Co., Georgia.

Anatomy. Discussed by Lea (1863: 415).

Habitat. Lives in muddy banks, or buried in sand in flowing water.

Remarks. Elliptio shepardiana (Lea) is a singular species and it can be confused with no other one. It is obviously related to *E. lanceolata* (Lea), but differs from it by being over three times as long as high, whereas *lanceolata* is just over twice as long as high. In *shepardiana* the anterior end is the widest part of the shell; it is almost always arcuate, and is consistently pointed. It replaces *E. lanceolata* in the main tributaries of the Altamaha River.

Range. Southern Atlantic Slope: restricted to the Altamaha River system, Georgia.

Specimens Examined

Altamaha River System

Ocmulgee River Drainage. *Georgia*: Ocmulgee River above Jackson, Butts Co. Big Tucsawhatchee Creek, 6 mi. S Hawkinsville, Pulaski Co. Ocmulgee River, Jacksonville; Ocmulgee River, 1 mi. S Lumber City; *both* Telfair Co. Oconee River Milledgeville, Baldwin Co. Oconee River, 2.5 mi. N Glenwood; Ochwalkee Creek, 2 mi. E Glenwood; *both* Wheeler Co.

Altamaha River Drainage. *Georgia*: Altamaha River, 7 mi. N Hazlehurst, Montgomery Co. Altamaha River, 10 mi. NE

Surrency, Appling Co. Altamaha River, 11 mi. N Odum; Altamaha River, "Riverside Park," 4 mi. N Jesup; *both* Wayne Co. Altamaha River, 3 mi. NE Everett City, Glynn Co. Altamaha River, near Fort Barrington; Penhollaway Creek, 5 mi. S Fort Barrington; Altamaha River, Hopeton, near Darien; *all* McIntosh Co.

Genus *Uniomerus* Conrad

Uniomerus Conrad 1853, Proc. Acad. Nat. Sci. Phila., 6: 268. Species listed: *U. declivis* Say, *camptodon* Say, *subcrocceus* Conrad, *sayii* Ward, *rivularis* Conrad, *porrectus* Conrad, *symmetricus* Lea, *excultus* Conrad.
Conrad, 1854, Jour. Acad. Nat. Sci. Phila., ser. 2, 2: 296.

Type species, *Unio tetralasmus* Say. Subsequent designation, Simpson, 1900, Proc. United States Natl. Mus., 22: 739. Since *U. excultus* Conrad is included in Simpson's synonymy of *U. tetralasmus*, the subsequent selection of the former by Clench and Turner, 1956, Bull. Florida State Mus., 1: 176, is invalid under Article 69 (a) (iv) of the Int. Code Zool. Nomen. (1964). Ortmann, 1912a, Ann. Carnegie Mus., 8: 272.

Frierson (1927: 34–35) lists a number of species and subspecies under *Uniomerus*. Like *Elliptio*, *Uniomerus* has a wide range of environmental tolerance, and while there are a number of ecophenotypes, the genus appears to be monotypic.

Uniomerus tetralasmus (Say)
Plate 12: 1–6

Unio tetralasmus Say, [September] 1831, American Conchology, no. 3 [no pagination] pl. 23 (Bayou St. John [not located] near New Orleans, Louisiana; type not in ANSP [lost]).

Unio obesus Lea 1831, Trans. Amer. Philos. Soc., 4: 96, 108, pl. 13, fig. 26 (York River, Virginia [corrected to Georgia; Maj. Leconte on p. 108]; figured holotype USNM 85366, labeled, "Little Ogeechee River [Hancock Co.], Georgia; Maj. Leconte"). Lea, 1834, Obs. Unio, 1: 106, 118. Clench and Turner, 1956, Bull. Florida State Mus., 1: 178, did not see the type, which has the corrected locality written on it, and unfortunately restricted the type locality to Columbus, Georgia.
Lea, 1854 (Proc. Acad. Nat. Sci. Phila., 7: 243), claimed that this description appeared during the latter part of 1831. It was reported on in 1832, (Jan.-March number of: Amer. Jour. Sci., 22: 169 [probably appeared in April]). There is no way to be sure which name has priority, but Say's name is certainly better known, and it is given primary status here without equivocation.

Unio declivis Say 1831 [1832], Transylvania Jour. Med., 4: 527 (Bayou Teche, Louisiana). Say, 1832, American Conchology, no. 4 [no pagination], pl. 35; three syntypes ANSP 41698 from Mr. Barabino, all smaller than figured type.

Unio camptodon Say 1832, American Conchology, no. 5 [no pagination], pl. 42 (opposite to New Orleans [Jefferson Parish, Louisiana], in ponds; type not in ANSP [lost]).

Unio geometricus Lea 1832, Trans. Amer. Philos. Soc., 5: 38, pl. 4, fig. 10 (Bayou Teche, Louisiana; figured holotype USNM 85712) Lea, 1834, Obs. Unio, 1: 150.

Unio blandingianus Lea 1834, Trans. Amer. Philos. Soc., 5: 101, pl. 15, fig. 44 (St. Johns River, Florida; figured holotype USNM 85715). Lea, 1834, Obs. Unio, 1: 213.

Unio declivis Conrad 1836 *non* Say. See under: *Unio rivularis* Conrad, 1853.

Unio excultus Conrad, 1838, Monography Unionidae, no. 11, p. 99, pl. 55, fig. 1 (New Orleans [Orleans Parish], Louisiana; type ANSP 20427 [lost]).

Unio sayii Ward 1839, [*in* Tappan], Amer. Jour. Sci., 35: 268, pl. 3, fig. 1 (Walnut Creek and Ohio Canal, near Circleville [Pickaway Co.], Ohio; type [location unknown]).

Unio paralellus [*sic*] Conrad 1841, Proc. Acad. Nat. Sci. Phila., 1: 20 *non* Sowerby 1840. Changed to:

Unio porrectus Conrad 1845, Jour. Acad. Nat. Sci. Phila., ser. 2, 2: 296, pl. 26, fig. 7 ([Pearl River] Jackson [Hinds Co.], Mississippi; figured holotype ANSP 42847).

Unio buddianus Lea 1843, Desc. Twelve Uniones (Lake George and Lake Monroe, Florida). Lea, 1845, Trans. Amer. Philos. Soc., 9: 277, pl. 40, fig. 5; figured holotype USNM 85606, from Lake George. Lea, 1848, Obs. Unio, 4: 35.

Unio symmetricus Lea 1845, Trans. Amer. Philos. Soc., 10: 73, pl. 4, fig. 11 (Red River, Alexandria [Rapides Parish] Louisiana; figured holotype USNM 85604). Lea, 1848, Obs. Unio, 4: 47.

Unio paludicolus Gould 1845, Proc. Boston Soc. Nat. Hist., 2: 53 (Florida Everglades; lectotype MCZ 169278, selected by Johnson, 1964, Bull. United States Natl. Mus., 239: 121, pl. 31, fig. 3).

Unio ineptus Lea 1852, Trans. Amer. Philos. Soc., 10: 261, pl. 15, fig. 12 (Abbeville District [Savannah River drainage], South Carolina;

figured holotype USNM 85326). Lea, 1852, Obs. Unio, 5: 17.

Unio hebes Lea 1852, Trans. Amer. Philos. Soc., 10: 267, pl. 18, fig. 21 (Oconee River, near Athens [Clarke Co.], Georgia; figured holotype USNM 85383). Lea, 1852, Obs. Unio, 5: 23.

Unio rivularis Conrad 1853, Proc. Acad. Nat. Sci. Phila., 6: 257. New name for *Unio declivis* Conrad 1836 *non* Say 1831, *in* Monography Unionidae, no. 5, p. 45, pl. 23, fig. 1 (small creek in Green Co., Alabama; figured holotype ANSP 42852).

Unio paludicolor Conrad 1853, Proc. Acad. Nat. Sci. Phila., 6: 254. Error for *U. paludicolus* Gould.

Unio subcroceus Conrad 1854, Jour. Acad. Nat. Sci. Phila., ser. 2, 2: 297, pl. 27, fig. 1 (one of the tributaries to Canadian River, Arkansas; type not in ANSP [lost]).

Unio manubius Gould 1855, Proc. Boston Soc. Nat. Hist., 5: 229 (Chihuahua, 60 mi. from Camp Ringgold = Río Agualeguas, 3 mi. NE General Treviño, Nuevo Leon [State, Mexico], *teste* Taylor, 1967, Veliger, 10: 154; holotype MCZ 169447, figured by Johnson, 1964, Bull. United States Natl. Mus., 239: 108, pl. 32, fig. 5).

Unio columbensis Lea 1857, Proc. Acad. Nat. Sci. Phila., 9: 31 (Creeks near Columbus [Muscogee Co.], Georgia). Lea, 1858, Jour. Acad. Nat. Sci. Phila., ser. 2, 4: 75, pl. 14, fig. 55; figured holotype USNM 85360. Lea, 1858, Obs. Unio, 6: 75.

Unio jamesianus Lea 1857, Proc. Acad. Nat. Sci. Phila., 9: 84 ([Pearl River] Jackson [Hinds Co.], Mississippi). Lea, 1858, Jour. Acad. Nat. Sci. Phila., ser. 2, 4: 53, pl. 6, fig. 35; figured holotype USNM 85365). Lea, 1858, Obs. Unio, 6: 52.

Unio plantii Lea 1857, Proc. Acad. Nat. Sci. Phila., 9: 171 (Flint River, near Macon [Co.], Georgia). Lea, 1859, Jour. Acad. Nat. Sci. Phila., ser. 2, 4: 192, pl. 21, fig. 76; figured holotype USNM 85005. Lea, 1859, Obs. Unio, 7: 10. [Known only from the holotype, which is a pathological specimen].

Unio cicur Lea 1861, Proc. Acad. Nat. Sci. Phila., 13: 39 (Little Ocmulgee River, Georgia). Lea, 1862, Jour. Acad. Nat. Sci. Phila., ser. 2, 5: 93, pl. 13, fig. 241; figured holotype USNM 85532. Lea, 1862, Obs. Unio, 8: 97.

Unio squalidus Lea 1863, Proc. Acad. Nat. Sci. Phila., 15: 192 (Neuse River, near Raleigh [Wake Co.]; Roanoke River, near Weldon [Halifax Co.]; Deep River; *all* North Carolina). Lea, 1866, Jour. Acad. Nat. Sci. Phila., ser. 2, 6: 22, pl. 7, fig. 20; figured holotype USNM 85376, from Roanoke River. Lea, 1867, Obs. Unio, 11: 26.

Unio electrinus Reeve 1865, Conch. Iconica, 16, *Unio*, pl. 25, fig. 121 (Hab. ? Cuming coll'n; type, British Museum (Nat. Hist.) [lost]).

Unio bisselianus Lea 1867, Proc. Acad. Nat. Sci. Phila., 15: 81 (Bissels Pond, Charlotte [Mecklenburg Co.], North Carolina). Lea, 1868, Jour. Acad. Nat. Sci. Phila., ser. 2, 6: 277, pl. 37, fig. 90; figured holotype USNM 85373. Lea, 1869, Obs. Unio, 12: 37.

Unio jewettii Lea 1867, Proc. Acad. Nat. Sci. Phila., 11: 81 (sink of Noonan's [Newnans] Lake [Alachua Co.], Florida). Lea, 1868, Jour. Acad. Nat. Sci. Phila., ser. 2, 6: 276, pl. 37, fig. 89; figured holotype USNM 85374. Lea, 1869, Obs. Unio, 12: 36.

Unio rivicolus Conrad 1868, Amer. Jour. Conch., 4: 280, pl. 18, fig. 4 (brook near Tampa [Hillsborough Co.], Florida; figured holotype ANSP 41411).

Unio pawensis Lea 1868, Proc. Acad. Nat. Sci. Phila., 20: 161 (Paw Creek [Mecklenburg Co.], Beaver Co. [= Creek, Gaston Co.], Catawba Run [Gaston and Mecklenburg Cos.]). Lea, 1868, Jour. Acad. Nat. Sci. Phila., ser. 2, 6: 302, pl. 45, fig. 114; figured holotype USNM 85380, labeled, "Beaver Creek, [into ?] Catawba Run, North Carolina." Lea, 1869, Obs. Unio, 12: 62.

Uniomerus obesus (Lea). Clench and Turner, 1956, Bull. Florida State Mus., 1: 177, pl. 5, fig. 2.

Description. Shell medium to large, reaching 114 mm in length. Outline rhomboid or long rhomboid. Valves subinflated or inflated, subsolid. Anterior end regularly rounded or slightly truncated; posterior end usually somewhat produced. Ventral margin slightly incurved. Dorsal margin slightly curved, generally forming a sharp angle with the almost straight posterior margin. Hinge ligament long and narrow, located posteriorly of the umbos. Posterior ridge rounded, ending in a point or feeble biangulation at the base of the shell, sometimes rendering older specimens a bit arcuate. Posterior slope often with two radial sulci. Umbos low to slightly elevated, located in the anterior quarter of the shell, their sculpture consisting of five or six heavy ridges that form a rounded angle on the posterior ridge, in front of which they tend to be corrugated. Periostracum generally black and slightly roughened, but with a satiny

sheen over most of the surface. Sometimes the surface is smooth and shiny, especially in the umbonal area, and may then be brownish yellow or yellowish mixed with green, not rayed.

Left valve with two ragged, subequal pseudocardinal teeth and two straight lateral teeth. Right valve with one triangular pseudocardinal often with a vestigial tooth above it; one lateral tooth. Beak cavities compressed, but with several muscle scars; anterior adductor muscle scars deep, posterior ones faint. Pallial line distinct. Nacre white, bluish white or pinkish to lurid purple.

Length mm	Height mm	Width mm	
114	61	39	Ogeechee River, Bartow, Jefferson Co., Georgia.
102	59	36	Little Cedar Creek, 1 mi. E Wrightsville, Jefferson Co., Georgia.
70	40	29	Richardson Creek, 2 mi. NE Thrift, Jenkins Co., Georgia.

Anatomy. Discussed by Lea (1863: 404).

Habitat. Generally lives in smaller streams and ponds on muddy bottoms, where it may be locally abundant. Sometimes found in sand with *Elliptio complanata* (Lightfoot) in larger Southern Atlantic Slope rivers, but in this habitat it is relatively scarce.

Remarks. In the Apalachicolan and Southern Atlantic Slope regions, *Uniomerus tetralasmus* (Say) can be confused with both *Elliptio complanata* (Lightfoot) and *E. icterina* (Conrad). In general, *tetralasmus* is more inflated than either of them, is proportionately higher, more acutely angular where the dorsal margin meets the posterior one, and very often has a satiny periostracum. The yellowish brown, unrayed periostracum and the bluish white or pinkish nacre of *tetralasmus* are distinct from the brown, often rayed periostracum and the dark purplish bronze nacre of *complanata.* The periostracum of *icterina* is sometimes bright yellow or chestnut, but like *complanata,* is generally rayed, though often but faintly, whereas *tetralasmus* scarcely ever appears rayed.

Uniomerus tetralasmus (Say) is generally common and abundant throughout the Apalachicolan region, Peninsular Florida, and in the Southern Atlantic Slope rivers of Georgia. It becomes noticeably scarce in the Carolinas. The periostracum is more inclined to be smooth on individuals from this northern end of the range.

Range. Interior Basin: Mississippi drainage generally, north to about latitude 40 degrees, Ohio River. West Gulf Coastal region, Alabama-Coosa River system, and Apalachicolan region: Rio Grande River system, Texas, east to the Suwannee River system, Florida. Peninsular Florida. Southern Atlantic Slope: Altamaha River system, north to the Nottoway River of the Chowan River system, North Carolina.

Specimens Examined

Altamaha River System

Ocmulgee River Drainage. *Georgia*: Swift Creek, SE Macon, Bibb Co. Mossy Creek, 3.5 mi. SW Kathleen, Houston Co. Tucsawhatchee [= Big] Creek, 5 mi. SW Hawkinsville; Cedar Creek, Fountains Mill, 7 mi. WSW Hawkinsville; Mosquito Creek, 8 mi. SE Hawkinsville; *all* Pulaski Co. Brushy Creek, 8 mi. NW Abbeville, Wilcox Co. House Creek, Bowens Mill, 9 mi. N Fitzgerald, Ben Hill Co.

Little Ocmulgee River Drainage. *Georgia:* Little Ocmulgee River, 6 mi. NE Cochran, Bleckley Co. Alligator Creek, 2.5 mi. SW Alamo, Wheeler Co. Gum Swamp Creek, 1 mi. N McRae, Telfair Co.

Oconee River Drainage. *Georgia*: Oconee River, near Athens, Clarke Co. (USNM). Black Creek, 7 mi. N McIntyre; Napiers Creek, 6 mi. N McIntyre; Ochee Creek, about 5 mi. SE Toomsboro; *all* Wilkinson Co. Rocky Creek, 6 mi. E Dudley; Turkey Creek, 6 mi. W Dublin; *both* Laurens Co. Ochwalkee Creek, 2 mi. E Glenwood, Wheeler Co.

Ohoopee River Drainage. *Georgia*: Ohoopee River, 4 mi. S Tennible, Washington Co. Little Ohoopee River, 10 mi. NE Wrightsville; Little Cedar Creek, 1 mi. E Wrightsville; Big Cedar Creek, 1 mi. SE Wrightsville; outlet of Rollins Pond, 2 mi. SE Wrightsville; Battleground Creek, 1 mi. N Kite; Dry Creek, 9 mi. NW Adrian; *all* Johnson Co. Pendleton Creek, 8 mi. N Soperton, Treutlen Co. Mulepen Creek, 2 mi. E Adrian; Yam Grande Creek, 3 mi. W Swainsboro; Little Ohoopee River, 6 mi. SW Swainsboro; *all* Emanuel Co.

Altamaha River Drainage. *Georgia*: Hopeton, near Darien, McIntosh Co. Brunswick, Glynn Co.

Ogeechee River System

Canoochee River Drainage. *Georgia*: Rocky Creek, 1.5 mi. E Swainsboro; Canoochee River, 4 mi. E Swainsboro; Little Canoochee Creek, 6 mi. E Swainsboro; *all* Emanuel Co. Little Lotts Creek, 2 mi. SE Statesboro; Lotts Creek, 7 mi. SW Statesboro; *both* Bulloch Co.

Ogeechee River Drainage. *Georgia*: Little Ogeechee River [Hancock Co.] (USNM). Ogeechee River, Bartow; Nails Creek, 2 mi. S Bartow; Rocky Creek, 2 mi. S Wadley; *all* Jefferson Co. Mill Creek, 5 mi. E Midville; Barkcamp Creek, 7 mi. E Midville; Barkcamp Creek, 9 mi. SW Waynesboro; *all* Burke Co. Spring, Ogeechee River, 1 mi. S Millen; Richardson Creek, 2 mi. NE Thrift; *both* Jenkins Co. Ogeechee River, Flat Ford Landing (MZUM); Dolly Lake, about 1.5 mi. below Kiterlighter Camp (MZUM); *both* Bryan Co.

Savannah River System

Savannah River Drainage. *South Carolina:* Abbeville District (USNM), Turkey Creek, 7 mi. NW Edgefield, Edgefield Co. *Georgia:* Beaverdam Creek, 7 mi. NW Girard; outlet of Waynesboro Lake, Waynesboro; Mill Race, 2 mi. N Sardis; *all* Burke Co. Brier Creek, 6 mi. N Sylvania, Screven Co. Savannah River, Atomic Energy Plant, 25 mi. S Augusta (ANSP). *South Carolina*: Savannah River, 2 mi. SW Millettville (ANSP); Savannah River, Kingjaw Point, 10 mi. WSW Allendale (ANSP); *both* Allendale Co. Mouth of Vermezobre Creek, Savannah Wildlife Reservation, Jasper Co. (MZUM). *Georgia*: Pond near Savannah, Chatham Co.

Combahee River System

Salkehatchie River Drainage. *South Carolina:* Lemon Creek, 5 mi. W Smoaks, Colleton Co.

Edisto River System

Edisto River Drainage. *South Carolina:* 20 mi. W Charleston, Charleston Co. Edisto River [not localized].

Cooper-Santee River System

Cooper River Drainage. *South Carolina:* Cooper River (USNM).

Catawba River Drainage. *North Carolina:* Beaver Creek, Gaston Co. Paw Creek; Irwins Creek; Bissels Pond, Charlotte; Elias Pond, 10 mi. from Charlotte; *all* Mecklenburg Co.

Wateree River Drainage. *South Carolina:* Wateree River, 2.5 mi. W Camden; Big Pine Tree Creek, 1.5 mi. S Camden; *both* Kershaw Co.

Santee River Drainage. *South Carolina:* Green Swamp Creek, 2.5 mi. W Sumter, Sumter Co. Poplar Creek, Schulers Fish Pond, near Santee State Park, Orangeburg Co. Santee River, Cross, Berkeley Co.

Black River System

Black River Drainage. *South Carolina*: Cowpen Swamp, 11 mi. NE Sumter, Sumter Co.

Pedee River System

Lynches River Drainage. *South Carolina:* Lynches River, 2 mi. NE Bishopville, Lee Co.

Yadkin River Drainage. *North Carolina:* Yadkin River.

Waccamaw River System

Waccamaw River Drainage. *North Carolina:* Lake Waccamaw (USNM); drainage canal beside Lake Waccamaw, 1 mi. NNW Duprec Landing; *both* Columbus Co. *South Carolina:* Waccamaw River, Wachesaw Landing, 2 mi. W Murrells Inlet, Georgetown Co.

Cape Fear River System

Deep River Drainage. *North Carolina*: Deep River (USNM).

Cape Fear River Drainage. *North Carolina:* Rocky River, Chatham Co. 11 mi. N Sanford, Lee Co. Stream below Greenfield Mill Pond, Wilmington, New Hanover Co. (ANSP).

Neuse River System

Neuse River Drainage. *North Carolina:* Neuse River, near Raleigh, Wake Co.

Pamlico River System

Tar River Drainage. *North Carolina*: Sandy Creek, Franklin Co. Fishing Creek, 4 mi. E Leggett; Tar River, Tarboro; *both* Edgecombe Co.

Roanoke River System

Roanoke River Drainage. *North Carolina*: Roanoke River, near Weldon, Halifax Co. (USNM).

Chowan River System

Nottoway River Drainage. *Virginia*: Nottoway River.

Subfamily **Anodontinae** (Swainson 1840) Ortmann 1910

Genus *Lasmigona* Rafinesque

Subgenus *Lasmigona s.s.* Rafinesque

Lasmigona Rafinesque 1831, Continuation of Monog. Bivalve Shells of River Ohio (Phila.), p. 4. Species listed: *Alasmidonta marginata* Say, *A. costata* Rafinesque.

Type species, *Alasmidonta costata* Rafinesque. Subsequent designation, Simpson 1900, Proc. United States Natl. Mus., 22: 664.

Symphynota Simpson 1900, Proc. United States Natl. Mus., 22: 662.

Type species, *Symphynota compressa* Lea, original designation, *non Symphynota* Lea 1829, the type species of which is *Unio alata* Say. Original designation.

There is only one species in *Lasmigona s. s.*, *L. costata* (Rafinesque), which is found in the Interior Basin and the upper St. Lawrence River system. In addition to the subgenera discussed here are *Alasminota* Ortmann (*Sulcularia* Rafinesque is not identifiable, *teste* Ortmann and Walker, 1922: 36) and *Pterosyna* Rafinesque. They do not occur on the Atlantic Slope, but belong to the Interior Basin.

Subgenus *Platynaias* Walker

Symphynota Simpson 1900, Proc. United States Natl. Mus., 22: 662. [*non*] Lea. (See under *Lasmigona*, above.)

Platynaias Walker 1918, Occ. Pap. Mus. Zool., Univ. Mich., 49: 2.

Type species, *Symphynota compressa* Lea, original designation.

Platynaias probably contains only two, probably allopatric species, *L. compressa* (Lea) (Ortmann 1919: 116, pl. 9, figs. 1, 2 as *L. viridis* Rafinesque), which is found in the Interior Basin, Hudson Bay; Upper Mississippi, Ohio, and St. Lawrence River systems from Saskatchewan and Nebraska to Vermont; extending into the Hudson River on the Atlantic Slope; and *L. subviridis* (Conrad), which is primarily a species of the Atlantic Slope, but which extends into the Lake Ontario drainage. Most of the other taxa listed under this subgenus by Frierson (1927: 20, 21) are included elsewhere in this paper in synonymy, save for *L. neglecta* (Lea) and *L. quadrata* (Lea) which are out of the scope of this paper.

Lasmigona (*Platynaias*) *subviridis* (Conrad)

Plate 12: 7–9
Plate 13: 1

Unio subviridis Conrad 1835, New Fresh Water Shells United States; appendix, p. 4, pl. 9, fig. 1 (Schuylkill River; Juniata River [Blair Co.];

figured holotype ANSP 2105 [lost]; creeks in Lancaster Co.; [*all* Pennsylvania]).

Unio viridis Conrad 1836, Monography Unionidae, no. 4, p. 35, pl. 17, fig. 1, *non* Rafinesque 1820.

Unio tappanianus Lea 1838, Trans. Amer. Philos. Soc., 6: 62, pl. 17, fig. 55 ([Frankstown Branch], Juniata River, near Hollidaysburg [Blair Co.]; figured holotype USNM 85240; Schuylkill [River]; and a small stream near Lancaster; [*all* Pennsylvania]). Lea, 1838, Obs. Unio, 2: 62.

Unio hyalinus Lea 1845, Proc. Amer. Philos. Soc., 4: 164 ([James River drainage], Richmond [Henrico Co.], Virginia). Lea, 1848, Trans. Amer. Philos. Soc., 10: 69, pl. 2, fig. 4; figured holotype USNM 86131. Lea, 1848, Obs. Unio, 4: 43.

Unio decoratus Lea 1852, Trans. Amer. Philos. Soc., 10: 257, pl. 13, fig. 6 (Abbeville District [Savannah River drainage] South Carolina; figured holotype USNM 83972). Lea, 1852, Obs. Unio, 4: 43.

Unio pygmaeus Lea 1852, Proc. Amer. Philos. Soc., 5: 52 (Abbeville District [Savannah River drainage] South Carolina). Lea, 1852, Trans. Amer. Philos. Soc., 10: 262, pl. 15, fig. 14; figured holotype USNM 85240. Lea, 1852, Obs. Unio, 5: 18.

Unio charlottensis Lea 1863, Proc. Acad. Nat. Sci. Phila., 15: 191 ([Sugar Creek], near Charlotte, Mecklenburg Co., North Carolina). Lea, 1866, Jour. Acad. Nat. Sci. Phila., ser. 2, 6: 8, pl. 2, fig. 5; figured holotype USNM 85402. Lea, 1867, Obs. Unio, 11: 12.

Unio pertenuis Lea 1863, Proc. Acad. Nat. Sci. Phila., 15: 193 (Neuse River, near [6 mi. E of] Raleigh [Wake Co.], North Carolina). Lea, 1866, Jour. Acad. Nat. Sci. Phila., ser. 2, 6: 8, pl. 2, fig. 4; figured holotype USNM 86139. Lea, 1867, Obs. Unio, 11: 12.

Unio insolidus Lea 1872, Proc. Acad. Nat. Sci. Phila., 24: 159 (Abbeville District [Savannah River drainage] South Carolina; Fredericksburg [Spotsylvania Co.], Virginia; Irwin's Creek, Mecklenburg Co., North Carolina). Lea, 1874, Jour. Acad. Nat. Sci. Phila., ser. 2, 8: 40, pl. 13, fig. 37; figured holotype USNM 83974 from Irwin's Creek, Lea, 1874, Obs. Unio, 13: 44.

Symphynota viridis (Conrad). Simpson, 1914, Cat. Naiades, 1: 484.

Symphynota charlottensis (Lea). Simpson, 1914, Cat. Naiades, 1: 484.

Symphynota decorata (Lea). Simpson, 1914, Cat. Naiades, 1: 486.

Unio pygmaeus (Lea). Simpson, 1914, Cat. Naiades, 2: 649.

Lasmigona (*Platynaias*) *subviridis* (Conrad). Ortmann, 1919, Mem. Carnegie Mus., 8: 121, pl. 9, figs. 3, 4. Ortmann and Walker, 1922, Occ. Pap. Mus. Zool. Univ. Michigan, no. 112, p. 35. Clarke and Berg, 1959, Cornell Univ. Exp. Sta. Mem. no. 367, p. 32, fig. 31.

Description. Shell generally small, seldom reaching over 55 mm in length. Outline subrhomboid or subovate. Valves subcompressed to slightly inflated, subsolid. Anterior end regularly rounded; posterior end more broadly rounded and biangulate near the base. Ventral margin almost straight or slightly curved. Dorsal margin straight, sometimes forming a winglike angle with the obliquely descending posterior margin. Hinge ligament prominent. Posterior ridge low, but double, ending near the base of the shell in a slight biangulation. Posterior slope sometimes slightly concave above the upper ridge. Umbos elevated above the hinge line, located anterior to the middle of the shell, their sculpture consisting of about four subnodulous bars, the first two subconcentric, the others deeply double-looped, anterior loops rounded, posterior ones angular with a few radial threads behind. The disk is smooth or slightly roughened by growth rests; periostracum yellowish or brownish green, occasionally olivaceous, subshining to dull, usually faintly rayed over the entire surface, darker on the posterior slope.

Hinge teeth well developed but rather delicate. Left valve with two lamellate, pseudocardinals that are directed forward and almost parallel to the hinge with a rudimentary interdental projection which fits into an interdental groove in the right valve; two long, straight, thin, lateral teeth. Right valve with one long pseudocardinal, directed forward, almost parallel to the hinge line; interdentum wide; one thin lateral tooth. Beak cavities shallow, containing dorsal muscle scars. Anterior adductor muscle scars distinct, posterior ones less so. Pallial line distinct anteriorly, where the shell may be slightly thickened.

Nacre bluish white and iridescent, sometimes pinkish, especially toward the umbonal cavities.

Length mm	Height mm	Width mm	
60	37	19	Abbeville District [Savannah River drainage], South Carolina. Holotype of *Unio decoratus* Lea.
30	18	11	As above. Holotype of *Unio pygmaeus* Lea.
116	56	38	Pfeiffers Pond, Charlotte, Mecklenburg Co., North Carolina (ANSP).
117	59	29	*Lasmigona compressa* (Lea). Small brook, Middlebury, Addison Co., Vermont.

Anatomy. Discussed by Ortmann (1911: 283). Glochidia are subtriangular, almost semicircular, with hooks. They measure 0.36 mm in length, 0.30 mm in height. The host fish is not known.

Breeding season. This hermaphroditic species is bradytictic, the breeding season beginning in August and lasting until June (Ortmann, 1919: 122).

Habitat. Usually found in gravel or sandy bottoms in medium or small streams, as well as canals and the pond areas of streams; seems to avoid large rivers.

Remarks. With its lamellate pseudocardinal teeth and characteristic rudimentary interdental projection in the left valve, *Lasmigona subviridis* (Conrad) is not confused with any other Atlantic Slope species, except in New York, where its distribution overlaps that of *Lasmigona compressa* (Lea) in the lower St. Lawrence and Hudson river systems. *L. compressa,* which is found abundantly in the Ohio-Mississippi drainage of the Interior Basin, has a rather heavy, compressed, trapezoidal shell, and the left valve has a well-developed interdental projection. *L. subviridis* has almost invariably a smaller, thinner, more delicate shell which is more inflated (see comparative measurements, above), and the interdental projection is rudimentary.

Ortmann (1919: 123) calls attention to some specimens of *L. subviridis* from Conococheague Creek, Greencastle, Franklin Co., Pennsylvania, remarkable for their large size. The largest one measured 63 mm in length, 38 mm in height, and 26 mm in width. Lea described a single giant specimen of this species under the name *Unio charlottensis,* from Sugar Creek, near Charlotte, Mecklenburg Co., North Carolina, part of the Catawba River drainage of the upper Cooper-Santee River system, which measured 112 mm in length. During the last century, a few additional giant specimens, as well as a number of smaller ones, were collected in Pfeiffers Pond, Charlotte, Mecklenburg Co., North Carolina, by C. M. Wheatley (ANSP and MCZ). The original label on the lot in the Academy of Natural Sciences of Philadelphia (ca. 1900) states that, "the pond from which they were taken has long since been filled in."

Ortmann (1913a: 371; 1919: 124) found *L. subviridis* to be especially abundant on the west side of the Alleghenian divide in the Greenbrier and New rivers of the upper Kanawha drainage in Virginia and West Virginia, where he suggested this species originated.

Range. Interior Basin: New and Greenbrier rivers of the upper Kanawha River drainage, Virginia and West Virginia. Atlantic Slope: upper Savannah River system, South Carolina; north to the Hudson River system, westward through the Mohawk River and Erie [now New York State Barge] Canal to the Genesee River; *all* New York.

Specimens Examined

Savannah River System

Savannah River Drainage. *South Carolina:* Abbeville District (USNM).

Cooper-Santee River System

Catawba River Drainage. *North Carolina:* Irwins Creek (MZUM); Sugar Creek,

near Charlotte (USNM); Pfeiffers Pond, Charlotte; *all* Mecklenburg Co. [Ten Mile Creek], Wolfsville [7 mi. W Monroe], Union Co. (MZUM).

Pedee River System

Yadkin River Drainage. *North Carolina:* Crosiers Branch, Cabarrus Co. (ANSP).

Cape Fear River System

Cape Fear River Drainage. *North Carolina:* Cape Fear River, Kinnon, Cumberland Co. (MZUM).

Neuse River System

Neuse River Drainage. *North Carolina*: Flat River, 2.5 mi. S Mt. Tirzah, Person Co. (80). Flat River, 2.3 mi. ENE Rougemont, Durham Co. (78). Eno River, 1.75 mi. ESE Hillsboro Center, Orange Co. (117). Neuse River, 9.5 mi. ENE Durham, Durham Co. (62). Neuse River, 5 mi. NNW Bayleaf (56); Neuse River, Falls (50); Neuse River, 5.75 mi. E Raleigh (45); Neuse River, 3 mi. S Milburnie (33); Stirrup Iron Creek, 2 mi. NE Morrisville (43); Swift Creek, 3 mi. SSW Garner (20); Little River, Tarpleys Mill, 2 mi. NE Wendell (5); *all* Wake Co. Neuse River, 3.5 mi. NNE Smithfield, Johnston Co. (25).

Pamlico River System

Tar River Drainage. *North Carolina*: Tar River, Providence, Granville Co. (MZUM). Tar River, 2 mi. W Springhope, Nash Co.

Roanoke River System

Roanoke River Drainage. *Virginia*: Stone River, Clarksville, Mecklenburg Co. (MZUM).

James River System

Appomattox River Drainage. *Virginia*: Appomattox River, Petersburg, Dinwiddie Co. (MZUM).

James River Drainage. *Virginia*: North River, Buena Vista, Rockbridge Co. (Ortmann, 1919: 124). Rivanna River, 2 mi. W Columbia, Fluvanna Co. James River, opposite Maidens, Goochland Co. [James River], Richmond, Henrico Co. (Lea).

York River System

North Anna River Drainage. *Virginia*: Church River, Orange Co. (MZUM).

Rappahannock River System

Rapidan River Drainage. *Virginia*: Rapidan River, 3 mi. N Orange, Orange Co. Rapidan River, Rapidan, Culpeper Co. (Ortmann, 1919: 124).

Rappahannock River Drainage. *Virginia:* Rappahannock River, Remington, Fauquier Co. (Ortmann, 1919: 124). [Rappahannock River], Fredericksburg, Spotsylvania Co. (Lea).

Potomac River System

Potomac River Drainage. *West Virginia:* Sleepy Creek, 8 mi. E Berkeley Springs, Morgan Co. (MZUM). *Virginia:* S. Fork, Shenandoah River, Elkton, Rockingham Co. (Ortmann, 1919: 124). *West Virginia:* S. Fork, Shenandoah River, Harpers Ferry, Jefferson Co. (Ortmann, 1919: 124). *Virginia:* Potomac River, 5 mi. S Lucketts, Loudoun Co. Potomac River, Great Falls County Park, Fairfax Co. (USNM).

Genus *Alasmidonta* Say
Subgenus *Prolasmidonta* Ortmann

Prolasmidonta Ortmann 1914, Nautilus, 28: 44. Type species, *Unio heterodon* Lea, original designation. This subgenus is monotypic.

Alasmidonta heterodon (Lea) is restricted to the Atlantic Slope region. The general shape and the distinct posterior ridge give the shell the unmistakable look of an *Alasmidonta,* but it is not close to the other members of the genus. There are two lateral teeth in the right valve and one in the left which is the reverse arrangement

of these teeth in all other Atlantic Slope Unionidae.

Alasmidonta (Prolasmidonta) heterodon (Lea)

Plate 13: 2

Unio heterodon Lea 1830, Trans. Amer. Philos. Soc., 3: 428, pl. 8, fig. 11 (Schuylkill [River] and Derby Creek [mostly in Delaware Co.], Pennsylvania; figured type, belonged to Mr. Mason, not in USNM or ANSP [presumed lost]. Lea mentions specimens in possession of T. A. Conrad, now ANSP 41004, 41005). Lea, 1834, Obs. Unio, 1: 42.

Alasmidonta heterodon (Lea) 1914, Simpson, Cat. Naiades, 1: 499.

Alasmidonta (Prolasmidonta) heterodon (Lea). Ortmann, 1919, Mem. Carnegie Mus., 8: 173, pl. 12, figs. 1, 2. Clarke and Berg, 1959, Cornell Univ. Exp. Sta. Mem. no. 367, p. 24, fig. 35.

Description. Shell small, generally from 30 to 45 mm, seldom reaching more than 50 mm in length. Outline subrhomboidal or subtrapezoidal, sometimes more or less elongate. Valves rather flat, though females are somewhat swollen in the region of the posterior ridge, thin but strong. Anterior end regularly rounded; posterior end somewhat produced and angular. Ventral margin straight or slightly arcuate. Dorsal margin short and straight, almost always forming a sharp angle with the obliquely descending posterior margin. Hinge ligament occupying almost all of the posterior dorsal margin. Posterior ridge distinct though broadly rounded, sometimes almost angular in females, usually ending in a broad point near the base. Posterior slope flat, or slightly concave, with one or two fine radiating lines. Umbos somewhat inflated but not very prominent, located slightly anterior to the middle of the shell, their sculpture consisting of three or four, sometimes five, bars, the first two concentric, the others with a distinct angle on the posterior ridge in front of which is a shallow sinus. The bars are rather heavy; the sinus does not assume the shape of a re-entering angle, and the sculpture can not be regarded as double-looped. The disk is smooth; the periostracum is greenish olive to brownish. In addition to indistinct concentric bands of lighter and darker green, there are often obscure green rays which are occasionally sharp and well defined.

Hinge teeth delicate. Left valve with two lamellate pseudocardinal teeth which are parallel to the hinge, the anterior one sometimes rudimentary; an interdental tooth that may be well developed and isolated or connected with the posterior pseudocardinal; one lateral tooth. Right valve with two compressed crenulated pseudocardinals, the more anterior one often rudimentary; interdentum narrow and short; two delicate lateral teeth, the upper one often partially rudimentary. Beak cavities shallow, containing dorsal muscle scars. Anterior adductor muscle scars distinct, posterior ones less so. Pallial line distinct anteriorly only. Nacre bluish or silvery white, often cream colored or yellowish toward the umbonal cavities.

Sexual differences are visible in the shell. In general the male shell is compressed, ovate, and elongate, with the ventral margin curved, the posterior ridge not sharp, and the posterior slope not truncate, whereas the female shell is swollen in the region of the posterior ridge, rendering the posterior slope truncate, the outline of the shell more trapezoidal, and the ventral margin slightly concave.

Length mm	Height mm	Width mm	
52	26	17	[Ten Mile River], Mixville, Cheshire, New Haven Co., Connecticut. Male.
40	23	16	Neuse River, Pooles Bridge, Wake Co., North Carolina. Male.
38	22	18	Little River, 2 mi. NE Wendell, Wake Co., North Carolina. Female.

Anatomy. Discussed by Lea (1863: 442) and Ortmann (1911: 295). Glochidia are subtriangular with strong hooks. They measure 0.30 mm in length, 0.25 mm in height. The host fish is unknown.

Breeding season. Ortmann (1919: 174) reports gravid females having been taken in February and April. It is bradytictic.

Habitat. Lives in water that does not flow very fast, in gravel, sand, or in muddy sand.

Remarks. Alasmidonta heterodon (Lea) is an Atlantic Slope species, not closely related to the other members of the genus. It can be confused with no other unionid in the region because of its distinct dentition. *A. heterodon* has two lateral teeth in the right valve, though the upper one may be rather rudimentary, and one in the left valve. This tooth arrangement is just the opposite of all other Atlantic Slope Unionidae.

This species is usually rare, and its erratic distribution may be merely a reflection of inadequate collecting. Judging from the available records, it appears to be most widely distributed and abundant in the Connecticut River system of Vermont, New Hampshire, Massachusetts, and Connecticut.

Range. Atlantic Slope: Neuse River system, North Carolina, north to the Petitcodiac River system, New Brunswick, Canada, but discontinuous. Known only from the following additional intervening drainage systems; Rappahannock River system, Virginia; Potomac River system, Maryland; Delaware River system, Pennsylvania; Housatonic River system, Connecticut (Linsley, 1845); Quinnipiac River system, Connecticut; Connecticut River system, Vermont, New Hampshire, Massachusetts, Connecticut; Merrimac River system, Massachusetts.

Specimens Examined

Neuse River System

Neuse River Drainage. *North Carolina*: Neuse River, Pooles Bridge [not located]; Neuse River [6 mi. E Raleigh]; Little River, Tarpleys Mill, 2 mi. NE Wendell (5); *all* Wake Co. Chicod Creek, Pitt Co. (MZUM).

Rappahannock River System

Rapidan River Drainage. *Virginia*: Blue Run, Orange Co. (MZUM).

Rappahannock River Drainage. *Virginia:* Mountain Run, Culpeper Co. (Ortmann, 1919: 175).

Potomac River System

Potomac River Drainage. *Maryland*: McIntosh Run, 4 mi. N Leonardtown, St. Marys Co. (H. D. Athearn).

Subgenus *Alasmidonta s.s.* Say

Monodonta Say 1817, Nicholson's Encyclopedia, 2 [no pagination] *non* Lamarck 1799.

Alasmidonta Say 1818, Jour. Acad. Nat. Sci. Phila., ser. 1, 1: 459.

Type species, *Monodonta undulata* Say. Monotypic.

Alasmodonta [*sic*] Say 1819, Nicholson's Encyclopedia, ed. 3, 4 [no pagination].

Hemiodon Swainson 1849, Treatise on Malacology, pp. 288, 381. Species listed: *H. undulatus* [Say], *An. rugosus, purpurascens, areolata* [*all* Swainson], *non Hemiodon* Swainson, *op. cit.*, p. 191.

Type species, *A. undulata* Say. Subsequent designation, Hermannsen, 1847, Indicis Generum Malacozoorum, 1: 527.

Uniopsis Swainson 1840, Treatise on Malacology, pp. 289, 382.

Type species, *U. mytiloides* Swainson and *U. radiata* Swainson. Both names are based on the same fig., no. 64 = *Alasmidonta undulata* (Say).

Bullella Simpson 1900, Proc. United States Natl. Mus., 22: 672.

Type species, *Margaritana arcula* Lea. Original designation.

Jugosus Simpson 1914, Cat. Naiades, 1: 357.

Type species, *Strophitus wrightianus* Walker. Original designation, Simpson, 1900, Proc. United States Natl. Mus., 22: 666. Ortmann, 1914, Nautilus, 28: 45.

Alasmidonta s. s. is restricted to the Apalachicolan and Atlantic Slope regions. There is one other species in this subgenus that is not covered in this paper, *A. wrightiana* (Walker) (Johnson, 1967: 8, pl. 2, fig. 5), from the Ochlockonee River system, Florida.

In addition to the subgenera discussed here, or placed in synonymy above, Frier-

son (1927: 18, 19) includes in his list two other subgenera of *Alasmidonta*, *Pressodonta* Simpson, which appears to be represented in the Interior Basin by a single species, *A. calceola* (Lea); and *Sulcularia* Rafinesque, which Ortmann and Walker (1922: 33) show is not identifiable. The species listed under it belong in the genus *Lasmigona*, subgenus *Alasminota* Ortmann.

Alasmidonta (*Alasmidonta*) *undulata* (Say)
Plate 13: 3–4

Unio undulata Say 1817, Nicholson's Encyclopedia, 2 [no pagination], pl. 3, fig. 3 (Delaware and Schuylkill rivers [near Philadelphia, Philadelphia Co., Pennsylvania]; type, not in ANSP [lost]).

Unio glabratus Sowerby 1823, Genera of Recent and Fossil Shells, no. 16, fig. 3 (no locality, type not in British Museum (Nat. Hist.) [lost]). *non* Lamarck 1819.

Alasmidonta sculptilis Say 1829, New Harmony [Indiana] Disseminator, 2, no. 22, p. 339 (Virginia; type not in ANSP [lost]).

Unio hians Valenciennes 1827, *in* Humboldt and Bonpland, Voyage aux Régions Equinoxiales du Nouveau Continent, Pt. 2, 2: 235, pl. 54, figs. 2a, b (environs de Philadelphie [Philadelphia Co., Pennsylvania]; type [location unknown]).

Uniopsis radiata Swainson 1840, Treatise on Malacology, p. 289, fig. 62 ([North America] type [location unknown]).

Uniopsis mytiloides Swainson 1840, Treatise on Malacology, p. 382, fig. 62 ([North America] type [location unknown]. [Both this and the preceding were found on the same figure.]

Unio swainsoni Sowerby 1868, Conch. Iconica, 16, *Unio*, pl. 76, fig. 396 (Hab. ? figured holotype British Museum [Nat. Hist.] 1900.3.19.21.).

Alasmidonta undulata (Say). Simpson, 1914, Cat. Naiades, 1: 494.

Alasmidonta (*Alasmidonta*) *undulata* (Say) Ortmann 1919, Mem. Carnegie Mus., 8: 117, pl. 11, fig. 7. Clarke and Berg, 1959, Cornell Univ. Exp. Sta. Mem. no. 367, p. 25, fig. 33. Athearn and Clarke, 1962, Natl. Mus. Canada, Bull. 183, p. 24, pl. 3, figs. 3, 4.

Description. Shell generally small, from 50 to 65 mm, though sometimes reaching 80 mm in length. Outline elliptical or subrhomboid. Valves somewhat inflated, thin, becoming quite solid anteriorly. Anterior end regularly rounded; posterior end rather broadly pointed. Ventral margin almost always slightly rounded. Dorsal margin short and straight, forming an angle with the obliquely descending posterior margin. Hinge ligament located posteriorly of the umbos, occupying most of the dorsal margin. Posterior ridge rounded, sometimes with a faint second ridge above it. Posterior slope slightly concave, sometimes with irregular oblique corrugations. Umbos rather inflated and somewhat raised above the hinge line, located anterior to the middle of the shell, their sculpture consisting of four or five strong ridges running nearly parallel to the growth lines. These ridges extend some distance on the disk, and posteriorly are angular, thickened, and raised. They are crossed by fine, wrinkled, radiating threads. In front of and behind the regular umbonal sculpture there are radiating lirae. Generally the entire surface of the shell is smooth, though occasionally slightly roughened, especially posteriorly; periostracum greenish, yellowish, reddish brown, with more or less distinct green to blackish rays of varying width over the entire surface. The posterior slope is often somewhat lighter than the rest of the shell, with finer and sharper rays. Older shells become blackish, but the rays are still visible through transmitted light.

Left valve with a compressed, sometimes stumpy pseudocardinal tooth, often with a rudimentary one in front; interdentum rather broad, occasionally with a visible but connected interdental tooth; lateral tooth barely distinct. Right valve with one rather high, chunky, subtriangular tooth; often with a broad interdentum; with just a trace of a lateral tooth. Beak cavities moderately deep with muscle scars under the hinge plate. Anterior adductor muscle scars deep, posterior ones faint. Pallial line distinct anteriorly where the shell is thickened. Nacre white, salmon pink, or reddish, iridescent posteriorly.

Sexual differences are not visible in the shell.

Length mm	Height mm	Width mm	
80	51	39	Tar River, Bruce, 9 mi. NW Greenville, Pitt Co., North Carolina.
72	45	31	Neuse River, Falls, Wake Co., North Carolina.
54	32	23	Nottoway River, 3 mi. E Rawlings, Brunswick Co., Virginia.

Anatomy. Discussed by Ortmann (1911: 296). Glochidia are moderately large with strong hooks. They measure 0.34 mm in length and 0.36 mm in height. The host fish is unknown.

Breeding season. Ortmann (1919: 178) states that this species is clearly bradytictic, with a short interim in June and July.

Habitat. Lives in water that does not flow very fast, in gravel or sand, appears to avoid mud.

Remarks. Alasmidonta undulata (Say), of the Atlantic Slope, is not closely related to any *Alasmidonta* of the Interior Basin. Its nearest relatives are *A. arcula* of the Altamaha River system, Georgia, and *A. triangulata* of the Apalachicolan and Southern Atlantic Slope regions; but both of these species are more triangular in outline, with sharper posterior ridges. *A. undulata* also resembles *A. wrightiana* (Walker) of the Ochlockonee River system, Florida, in shape, and it has a similar tooth structure and rounded posterior ridge, but *wrightiana* has strong ridges which cover the posterior slope, whereas *undulata* is unsculptured.

A. undulata is a common species, especially on the Northern Atlantic Slope, and is often locally abundant. It seems to be somewhat less common on the Southern Atlantic Slope. It avoids the larger rivers, preferring smaller streams, in which it often goes far up toward the headwaters.

Range. Atlantic Slope: Catawba River, North Carolina, of the upper Cooper-Santee River system, north to the lower St. Lawrence River system, Canada.

Specimens Examined

Cooper-Santee River System

Catawba River Drainage. *North Carolina:* Catawba River (USNM).

Pedee River System

Yadkin River Drainage. *North Carolina:* Uwhairie River (USNM).

Cape Fear River System

Cape Fear River Drainage. *North Carolina:* Morgan Creek, 1 mi. SE Chapel Hill, Orange Co. (MZUM). Rocky River, 11 mi. N Sanford, Chatham Co. (MZUM). Cape Fear River (MZUM).

Neuse River System

Neuse River Drainage. *North Carolina*: Neuse River, Falls (50); Neuse River, 5.75 mi. E Raleigh Center (45); Swift Creek, 3 mi. SSW Garner (20); Middle Creek, 6.25 mi. SE Apex (18); Little River, Tarpleys Mill, 2 mi. NE Wendell (5); *all* Wake Co.

Pamlico River System

Tar River Drainage. *North Carolina*: Tar River, Old Sparta, 3.5 mi. W Pinetops, Edgecomb Co. Tar River, Bruce, 9 mi. NW Greenville, Pitt Co.

Chowan River System

Nottoway River Drainage. *Virginia*: Nottoway River, 3 mi. E Rawlings, Brunswick Co.

James River System

James River Drainage. *Virginia*: Calfpasture River (Conrad, 1846: 407); North [= Maury] River, 2 mi. WNW Lexington (MZUM); North River, Buena Vista (USNM); *all* Rockbridge Co. Rivanna River, 2 mi. W Columbia, Fluvanna Co. James River, opposite Maidens, Goochland Co.

York River System

North Anna River Drainage. *Virginia*: Mine Run, Orange Co. (MZUM).

Rappahannock River System

Rapidan River Drainage. *Virginia*: Blue Run (MZUM); Mountain Run (MZUM); *both* Orange Co.

Rappahannock River Drainage. *Virginia:* Rappahannock River, Remington; Marsh Run, Remington (*both* Ortmann, 1919: 180); *both* Fauquier Co.

Occoquan Creek System

Occoquan Creek Drainage. *Virginia*: Broad Run [Fairfax Co.], 3 mi. W Manassas, Prince William Co.

Potomac River System

Potomac River Drainage. *Maryland*: Wills Creek, Ellerslie, Allegany Co. (Ortmann, 1919: 179). Potomac River, Hancock, Washington Co. (Ortmann, 1919: 179). *Pennsylvania:* Great Tonoloway Creek, Thompson Township, Fulton Co. (Ortmann, 1919: 179). Conococheague Creek, Greencastle and Scotland, Franklin Co. (Ortmann, 1919: 179). *Virginia:* N Fork, Shenandoah River, Broadway, Rockingham Co. (Ortmann, 1919: 179). S River of S Fork, Shenandoah River, Waynesboro, Augusta Co. (Ortmann, 1919: 179). S Fork, Shenandoah River, Elkton, Rockingham Co. Ortmann, 1919: 179). *West Virginia:* Shenandoah River, Harpers Ferry, Jefferson Co. (USNM). *Virginia:* Potomac River, Great Falls, Fairfax Co.

Alasmidonta (Alasmidonta) triangulata (Lea)

Plate 13: 5, 6

Margaritana triangulata Lea 1858, Proc. Acad. Nat. Sci. Phila., 10: 138 (Upper Chattahoochee [River], Georgia; Columbus, Georgia; Polato Co. [*sic*] [Potato Creek, Upson Co.], Georgia; Sawney's Creek [about 8 mi. NW Camden, Kershaw Co.], South Carolina). Lea, 1859, Jour. Acad. Nat. Sci. Phila., ser. 2, 4: 228, pl. 32, fig. 111; figured holotype USNM 86249, from Upper Chattahoochee [River], Lea, 1859, Obs. Unio, 7: 46.

Alasmidonta triangulata (Lea). Simpson, 1914, Cat. Naiades, 1: 509. Clench and Turner, 1956, Bull. Florida State Mus., 1: 180, pl. 5, fig. 4.

Strophitus wrightianus Clench and Turner 1956, Bull. Florida State Mus., 1: 180 *non* Walker 1901, Nautilus, 15: 65, pl. 3.

Description. Shell generally small, though reaching 70 mm in length in the Apalachicola River system. Outline subtriangular. Valves inflated, thin to rather solid. Anterior end regularly rounded; posterior end rather broadly pointed. Ventral margin almost always slightly rounded. Dorsal margin short and straight, forming an angle with the obliquely descending posterior margin. Hinge ligament occupying almost all of the posterior dorsal margin. Posterior ridge high and angular with a second or third faint ridge above it, the second one ending in a slight biangulation near the base of the shell. Umbos full and high, located anterior to the center of the shell, their sculpture consisting of a number of strong ridges running nearly parallel to the growth lines. These ridges extend some distance on the disk and are crossed by fine, wrinkled, radiating threads. In front of and behind the regular umbonal sculpture there are radiating lirae. The disk is smooth; the periostracum is usually fine and limited to the posterior slope. Young shells may be yellowish or greenish yellow, often with dark green rays of varying width. Older shells become dark brownish black, but the rays and yellowish ground color are still visible when seen through transmitted light.

Left valve with a compressed, sometimes stumpy pseudocardinal tooth, often with a rudimentary one in front; interdentum broad, occasionally with a visible but connected interdental tooth; lateral tooth barely visible. Right valve with one rather high subtriangular tooth; broad interdentum; lateral tooth barely visible. Beak cavities deep, with dorsal muscle scars under the hinge plate. Anterior adductor muscle scars deep, posterior ones faint.

Pallial line distinct anteriorly where the shell is thickened. Nacre bluish white to salmon pink.

Sexual differences are not visible in the shell.

Length mm	Height mm	Width mm	
68	47	38	Savannah River [Johnsons Landing], 10 mi. W Allendale, Allendale Co., South Carolina (MZUM).
48	32	27	Mill Race, 2 mi. N Sardis, Burke Co., Georgia.

Habitat. Prefers sandy mud in rocky pools and eddies of large creeks and rivers.

Remarks. Alasmidonta triangulata (Lea) of the Apalachicolan and Southern Atlantic Slope regions cannot be confused with *A. arcula* (Lea) of the Altamaha River system because it is proportionally not as high. The umbos are anterior to the center, and while incurved, do not render the hinge line concave, and the posterior ridge is not as acutely sharp.

A. triangulata is closest to *A. undulata* (Say) of the Atlantic Slope region, but the latter has a shape which is usually an elongated oval, a very broadly rounded posterior ridge, more ponderous pseudocardinals, and more of an interdentum. In the Apalachicolan region, *A. triangulata* can be confused only with *A. wrightiana* (Walker); the latter has the shape, rounded posterior ridge, and tooth structure of *A. undulata*, differing from *undulata* and *triangulata* in the strong ridges which cover the posterior slope.

A. triangulata is a rare species throughout its range, but is especially so on the Southern Atlantic Slope where each of the lots examined consists of only one or two specimens.

Range. Apalachicolan region: restricted to the Apalachicola River system. Southern Atlantic Slope: Ogeechee and Savannah river systems, Georgia; and Cooper-Santee River system, South Carolina.

Specimens Examined

Ogeechee River System

Ogeechee River Drainage. *Georgia*: Ogeechee River, Scarboro (MZUM); Ogeechee River, bridge, 1 mi. S Dover; *both* Screven Co. (MZUM).

Savannah River System

Savannah River Drainage. *South Carolina:* Savannah River [Johnsons Landing], 10 mi. W Allendale, Allendale Co. (MZUM). *Georgia:* Mill Race, 2 mi. N Sardis, Burke Co.

Cooper-Santee River System

Wateree River Drainage. *South Carolina:* Sawney's Creek [about 8 mi. NW Camden, Kershaw Co.] (USNM).

Alasmidonta (Alasmidonta) arcula (Lea)

Plate 13: 7, 8

Margaritana arcula Lea 1836, Synopsis Naiades, p. 43 [*nomen nudum*]. Lea, 1838, Trans. Amer. Philos. Soc., 6: 71, pl. 22, fig. 69 (Altamaha [River], Liberty [now Long] Co., Georgia; figured holotype USNM 86170). Lea, 1838, Obs. Unio, 2: 71.

Alasmidonta arcula (Lea). Simpson, 1914, Cat. Naiades, 1: 508.

Description. Shell medium, reaching 75 mm in length. Outline triangular. Valves much inflated, thin but strong. Anterior end regularly rounded; posterior end sharply truncated. Ventral margin straight or slightly rounded. Dorsal margin short and curved, forming a sharp angle with the obliquely truncated posterior margin. Hinge ligament occupying almost all of the posterior dorsal margin. Posterior ridge high and sharply angular, with a second faint ridge above, ending in a slight biangulation near the base of the shell. Posterior slope very truncated. Umbos extremely full and high, located at the center of the shell, their sculpture consisting of a number of strong ridges running nearly parallel to the growth lines. These ridges extend well out on the disk and

posteriorly are angular, considerably thickened, and raised. They are crossed by fine, wrinkled, radiating threads. In front of and behind the regular umbonal sculpture there are radiating lirae. The disk is smooth; the periostracum is usually fine and limited to the posterior slope. Shell dull greenish yellow with distinct green rays of varying length over the entire surface. Mature shells are often blackish, but the rays are still visible through transmitted light.

Left valve with a long compressed pseudocardinal tooth, often with a rudimentary one in front; interdental tooth distinct but connected; lateral teeth barely visible. Right valve with one compressed, triangular tooth; scarcely any interdentum; lateral tooth barely visible. Beak cavities very deep, with dorsal muscle scars under the hinge plate. Anterior adductor muscle scars deep, posterior ones faint. Pallial line distinct anteriorly where the shell is thickened. Nacre bluish white or white.

Sexual differences are not visible in the shell.

Length mm	Height mm	Width mm	
80	60	50	Altamaha River [Long Co.], Georgia.
67	51	44	Ocmulgee River, Hawkinsville, Pulaski Co., Georgia.
50	43	38	Altamaha River, 4 mi. NE Jesup, Wayne Co., Georgia.

Anatomy. Discussed by Lea (1863: 447).

Habitat. Lives in sandy mud below sand bars in sluggish water and eddies.

Remarks. Alasmidonta arcula (Lea) of the Altamaha River system cannot be confused with any other unionid in the Atlantic Slope region, though it is close to *A. triangulata* (Lea), which is found in both the Apalachicolan and Atlantic Slope regions. *Alasmidonta arcula* differs from *triangulata* by being proportionally higher with centrally located umbos which are so elevated as to be incurved, by its concave hinge line, and by its extremely sharp posterior ridge which forms almost a 90° angle with the posterior slope.

This is a rare species; not more than a few specimens have ever been collected at any station in this century save for a series of twenty-two specimens collected by H. D. Athearn in 1962 in the Ocmulgee River, below Lumber City, Telfair Co., Georgia. The old unlocalized specimens of *arcula* in the major museums are presumed to have been collected near the type locality in the tidewater region of the Altamaha River, where it may be, or was, more abundant.

Range. Southern Atlantic Slope: restricted to the Altamaha River system, Georgia.

Specimens Examined

Altamaha River System

Ocmulgee River Drainage. *Georgia*: Ocmulgee River, Hawkinsville; Limestone Creek, near Hartford (H. D. Athearn); *both* Pulaski Co. Ocmulgee River, below Lumber City, Telfair Co. (H. D. Athearn).

Ohoopee River Drainage. *Georgia*: Ohoopee River, 3 mi. N Leman, Emanuel Co.

Altamaha River Drainage. *Georgia*: Altamaha [River], Liberty [now Long] Co. (USNM). Altamaha River, Fort Barrington, McIntosh Co. (ANSP).

Subgenus *Decurambis* Rafinesque

Decurambis Rafinesque 1831, Continuation of Monograph Bivalve Shells of River Ohio (Phila.), pp. 4, 5. Species listed: *Alasmodon scriptum* Rafinesque and *A. atropurpureum* Rafinesque.

Type species, *Alasmodon scriptum* Rafinesque = *Alasmidonta marginata* (Say). Subsequent designation, Ortmann and Walker, 1922, Occ. Pap. Mus. Zool., Univ. Mich., no. 112, p. 38.

Rugifera Simpson 1900, Proc. United States Natl. Mus., 22: 670.

Type species, *Alasmidonta marginata* Say. Original designation.

The present author follows Ortmann and Walker (1922: 38) and regards *Decuram-*

bis as a subgenus of *Alasmidonta*, though Frierson (1927: 21) raised *Decurambis* to a genus.

Decurambis includes but two allopatric species: *A. marginata* Say (Ortmann, 1919: 181, pl. 12, fig. 3), primarily a species of the Interior Basin, but which is also found on the Northern Atlantic Slope in the Susquehanna and upper St. Lawrence drainage systems; and *A. varicosa* (Lamarck), which is limited in distribution to the Atlantic Slope.

Alasmidonta (Decurambis) varicosa (Lamarck)
Plate 14: 1, 2

Unio varicosa Lamarck 1819, Hist. Nat. des Animaux sans Vertèbres, 6: 78 (la rivière de Schuglkill [Schuylkill] près de Philadelphie [Philadelphia Co., Pennsylvania]; holotype, Geneva Museum. *teste* Johnson, 1953, Nautilus, 66: 95; aussi dans le lac Champlain, [Vermont]).

Alasmodon corrugata De Kay 1843, Zool. New York, Moll., pt. 5: 198, pl. 24, fig. 259 (Passaic River, New York; type, New York Lyceum of Nat. Hist. [destroyed by fire]).

Mya rugulosa Wood 1856, *in* Hanley, Index Test, p. 199, pl. 1 supp., fig. 7 (North America; type [probably lost]).

Alasmidonta varicosa (Lamarck). Simpson, 1914, Cat. Naiades, 1: 506.

Alasmidonta (Decurambis) varicosa (Lamarck). Ortmann, 1919, Mem. Carnegie Mus., 8: 190, pl. 12, fig. 5. Clarke and Berg, 1959, Cornell Univ. Exp. Sta. Mem. no. 367, p. 28, fig. 34. Athearn and Clarke, 1962, Natl. Mus. Canada, Bull. 183, p. 25, pl. 3, figs. 5, 6.

Description. Shell usually small, from 40 to 65 mm, though sometimes reaching 80 mm in length. Outline rhomboid or subelliptical. Valves not much inflated, thin but strong. Anterior end regularly rounded; posterior end slightly elongated and biangulate. Ventral margin straight or slightly arcuate. Dorsal margin straight, forming an indistinct angle with the obliquely descending posterior margin. Hinge ligament located posteriorly of the umbos, short but prominent. Posterior ridge broadly rounded, with a second very faint ridge above it, ending in a biangulation near the base. Posterior slope broadly rounded, with a system of fine radial wrinkles running to the upper posterior margin. Umbos large and somewhat inflated, but not high, located in the anterior third of the shell, their sculpture consisting of three or four thick bars. The disk is smooth; the periostracum is yellowish, greenish, brownish, or blackish, generally with distinct narrow or wide, straight, greenish or blackish rays. The rays are usually broken by growth lines.

Each valve has one thin, distinct, depressed, triangular pseudocardinal; no lateral teeth. Beak cavities moderately deep with muscle scars under the hinge plate; anterior adductor muscle scars deep, posterior ones less so. Pallial line distinct anteriorly where the shell is slightly thickened. Nacre bluish white, often with salmon, pinkish, or purplish shades.

Sexual differences are visible in the shell; females are slightly more swollen in the region of the posterior ridge. Occasionally the swelling is so great that the lateral faces of the shell in front of the ridge appear flat or even concave. The ventral margin may be slightly emarginate, but male shells are also sometimes emarginate so that the sex can not always be ascertained from the shell alone.

Length mm	Height mm	Width mm	
73.0	40.0	31.0	N Fork, Shenandoah River, E Woodstock, Shenandoah Co., Virginia. Female.
44.0	26.0	18.0	Turkey Creek, 8 mi. NW Edgefield, Edgefield Co., South Carolina. Female.
33.0	28.0	12.0	Rocky River, 11 mi. N Sanford, Chatham Co., North Carolina. Male.
32.0	29.5	13.0	As above. Female.

Anatomy. According to Ortmann (1919: 191), the anatomy of this species is very similar to that of *Alasmidonta marginata* Say.

Breeding season. Ortmann (1919: 191) found that in Pennsylvania breeding begins

in August, when eggs are present; glochidia are found in September, and are carried over the winter and discharged the following May.

Habitat. Lives among rocks on gravel substrates; also on sandy shoals, especially in rapids and riffles of small rivers and creeks.

Remarks. Alasmidonta varicosa (Lamarck), having rudimentary pseudocardinals, a lack of lateral teeth, and radial wrinkles on the posterior slope, is distinguishable from the other *Alasmidonta* of the Atlantic Slope region. It is replaced in the upper Tennessee and Cumberland river systems by *A. ravenelina* (Lea) which differs from *varicosa* by being more elongate, by having a more broadly biangulate posterior ridge, and by usually not having more than a trace of radial wrinkles on the posterior slope.

Alasmidonta varicosa is the Atlantic replacement of *A. marginata* Say which is found in the Interior Basin throughout the upper Mississippi drainage, including the Ohio, Tennessee and Cumberland river systems. In the Northern Atlantic Slope region, *marginata* is found in the Susquehanna River, Pennsylvania, and the upper St. Lawrence River, Canada. *A. marginata* has a very sharp posterior ridge and a truncated posterior slope, which renders the shell subtrapezoidal; also, the rays tend to be broken into spots. *A. varicosa* has a gradually rounded, broadly biangulate posterior ridge, a gently rounded posterior slope, and a rhomboidal shape. The rays are never broken into spots; the shell is not as heavy, nor does it grow as large as does *marginata*. Though *marginata* prefers larger rivers while *varicosa* prefers smaller streams, they are nevertheless sometimes found together where their ranges overlap, but they are easily separated.

Simpson (1914, 1: 506) correctly recorded this species from as far south as South Carolina, but I was unable to find the material on which his record was based. Ortmann (1919: 193) personally collected *A. varicosa* in the upper Catawba River, North Carolina, and Clench and Okkelberg collected a single specimen in 1929 in a tributary of the Savannah River, South Carolina. Seemingly rare below the Potomac River, Maryland, *A. varicosa* is relatively abundant on the Northern Atlantic Slope.

Range. Atlantic Slope: tributary of the upper Savannah River system, South Carolina, north to the lower St. Lawrence River system, Canada.

Specimens Examined

Savannah River System

Savannah River Drainage. *South Carolina:* Turkey Creek, 8 mi. NW Edgefield, Edgefield Co. (MZUM).

Cooper-Santee River System

Catawba River Drainage. *North Carolina:* Catawba River, Bridgewater, Burke Co. (Ortmann, 1919: 193).

Cape Fear River System

Cape Fear River Drainage. *North Carolina:* Rocky River, 11 mi. N Sanford, Chatham Co.

James River System

James River Drainage. *Virginia*: Calfpasture River (Conrad, 1846: 407 as *A. marginata* Say).

Occoquan Creek System

Occoquan Creek Drainage. *Virginia*: Broad Run [Fairfax Co.], 3 mi. W Manassas, Prince William Co.

Potomac River System

Potomac River Drainage. *Virginia*: N Fork, Shenandoah River, E Woodstock, Shenandoah Co. S Fork, Shenandoah River, Riverton, Warren Co. *Maryland:* Potomac River, Hancock, Washington Co. (Ortmann, 1919: 193).

Genus *Anodonta* Lamarck
Subgenus *Anodonta s.s.* Lamarck

Anodonta Lamarck 1799, Mémoires de la Soc. d'Hist. Nat. de Paris, p. 87.

Type species, *Mytilus cygneus* Linnaeus. Monotypic. Placed on the Official List of Generic Names in Zoology, in 1926, Opinion 94. Reconfirmed, 1959, Opinions and Declarations rendered by Int. Comm. Zool. Nomen., 20 (28): 303–10, Opinion 561.

Ortmann, 1912, Ann. Carnegie Mus., 8: 286, *partim*. *Anodonta s. s.* is found primarily in the Palearctic region of Europe and Asia and like the type species may be monoecious and have flat umbones. The several western American species of the Pacific region clearly belong to *Anodonta s. s.*

Subgenus *Pyganodon* Crosse and Fischer

Pyganodon Crosse and Fischer 1894, *in* Fischer and Crosse, Mission Sci. au Mexique, pt. 7, 2: 518. Species listed: *A. globosa* Lea; *A. tabascens* Morelet; *A. nopalatensis* Sowerby; *A. grijalvae* Morelet; *A. glauca* Valenciennes. Introduced as a section.

Type species, *Anodonta globosa* Lea. Subsequent designation, Frierson, 1927, Check List North American Naiades, p. 9, *teste* Errata et Corrigenda. Raised to a subgenus.

Frierson (1927: 14–16) used *Pyganodon* as a subgenus to include most of the *Anodonta* of middle and eastern North America.

It is suspected that when the Interior Basin taxa included in this subgenus are revised, it will be found that there are about an equal number of species in the Interior Basin and Atlantic Slope region.

Anodonta (Pyganodon) cataracta cataracta Say
Plate 14: 3, 4
Plate 15: 1

Anodonta fluviatilis Gmelin, of authors. See note under *Lampsilis ochracea* Say, p. 388.

Anodonta cataracta Say 1817, Nicholson's Encyclopedia, 2 [no pagination], pl. 3, fig. 2 (deep part of a mill dam [presumably near Philadelphia, Philadelphia Co., Pennsylvania, and here so restricted]; type, ANSP [lost]). Simpson, 1914, Cat. Naiades, 1: 386. Ortmann, 1919, Mem. Carnegie Mus., 8: 152, pl. 10, fig. 5, pl. 11, fig. 1. Clarke and Berg, 1959, Cornell Univ. Exp. Sta. Mem. 367, p. 39, fig. 46. Athearn and Clarke, 1962, Natl. Mus. Canada Bull. no. 183, p. 27, pl. 2, figs. 5, 6.

Anodonta marginata Say 1817, Nicholson's Encyclopedia, 2 [no pagination], pl. 3, fig. 5 (very common in our rivers [presumably near Philadelphia, Philadelphia Co., Pennsylvania, and here so restricted]; type, ANSP [lost]). Simpson, 1914, Cat. Naiades, 1: 388 [*partim*]. The measurements in the description, as transcribed into millimeters, indicate the type to have been 51 mm in length and 38 mm in height. The figured shell was 69 mm in length and 36 mm in height. The first set of dimensions are those of a *cataracta* from a creek environment, while the second are of the elongated form which is sometimes found in ponds, and which becomes more common in the northern range of *cataracta*.

Anodonta teres Conrad 1834, New Fresh Water Shells United States, p. 47, pl. 7, fig. 2 (Santee Canal [Berkeley Co.], South Carolina [type, ANSP lost]). Simpson, 1914, Cat. Naiades, 1: 390.

Anodon excurvata De Kay 1843, Zool. of New York, Moll., pt. 5, p. 202, pl. 17, fig. 233 (Shaker Pond, Niskayuna, Albany Co., New York; Passaic River [Paterson, Passaic Co., New Jersey]; type, New York State Colln., now in USNM [not yet located]).

Anodonta virgulata Lea 1857, Proc. Acad. Nat. Sci. Phila., 9: 86 (Roanoke River, Weldon [Halifax Co.], North Carolina; Washington Co., Georgia). Lea, 1862, Jour. Acad. Nat. Sci. Phila., ser. 2, 5: 213, pl. 33, fig. 282; figured holotype USNM 86593 from Roanoke River. Lea, 1863, Obs. Unio, 9: 35.

Anodonta lacustris Lea 1857, Proc. Acad. Nat. Sci. Phila., 9: 84 (Crooked Lake and Little Lakes [Herkimer Co.], New York). Lea, 1860, Jour. Acad. Nat. Sci. Phila., ser. 2, 4: 363, pl. 62, fig. 188; figured type USNM [not located]; though a slightly smaller specimen, USNM 86597 marked Mohawk, New York, ex Lewis, is labeled holotype. Lea, 1860, Obs. Unio, 8: 45.

Anodonta hallenbeckii Lea 1858, Proc. Acad. Nat. Sci. Phila., 10: 138 (Uphaupee [Uphapee] Creek, Macon Co., Georgia [Alabama]). Lea, 1859, Jour. Acad. Nat. Sci. Phila., ser. 2, 4: 50, pl. 32, fig. 112; figured holotype USNM 86428. Lea, 1859, Obs. Unio, 7: 50. Simpson, 1914, Cat. Naiades, 1: 392. Clench and Turner, 1956, Bull. Florida State Mus., 1: 186, pl. 9, fig. 1.

Anodonta gesneri Lea, 1858, Proc. Acad. Nat. Sci. Phila., 10: 139 (Uphaupee [Uphapee] Creek, Macon Co., Georgia [Alabama]). Lea, 1859, Jour. Acad. Nat. Sci. Phila., ser. 2, 4:

231, pl. 31, fig. 109; figured holotype USNM 86427. Lea, 1859, Obs. Unio, 7: 49.

Anodonta dariensis Lea 1858, Proc. Acad. Nat. Sci. Phila., 10: 139 (Hopeton, near Darien [McIntosh Co.]; Swift Creek, near Macon [Bibb Co.]; Flint River; *all* Georgia). Lea, 1859, Jour. Acad. Nat. Sci. Phila., ser. 2, 4: 230, pl. 28, fig. 99; figured holotype USNM 86600 from Swift Creek. Lea, 1859, Obs. Unio, 7: 48. Simpson, 1914, Cat. Naiades, 1: 394.

Anodonta williamsii Lea 1862, Proc. Acad. Nat. Sci. Phila., 14: 169 (Potomac River at the White House [District of Columbia]; below Mount Vernon [Fairfax Co., Virginia]; Othcalooga Creek [Gordon Co.], Georgia. Lea, 1866, Jour. Acad. Nat. Sci. Phila., ser. 2, 6: 27, pl. 10, fig. 26; type, USNM [not located]. Lea, 1867, Obs. Unio, 11: 31.

Anodonta tryoni Lea 1862, Proc. Acad. Nat. Sci. Phila., 14: 169 (Schuylkill River above Philadelphia; Delaware River at League Island [*both* Philadelphia Co., Pennsylvania]; Flemington [= Farmington, Hartford Co.], Connecticut; Westfield [Hampden Co.], Massachusetts; Potomac River near Chain Bridge, above Washington, D. C.). Lea, 1866, Jour. Acad. Nat. Sci. Phila., ser. 2, 6: 28, pl. 10, fig. 27; type, USNM [not located], paratype, USNM 86572 from Potomac River. Lea, 1867, Obs. Unio, 11: 32.

Anodonta dolearis Lea 1863, Proc. Acad. Nat. Sci. Phila., 15: 193 (Stewart's Mill Dam, Union Co., North Carolina). Changed to:

Anodonta doliaris Lea 1866, Jour. Acad. Nat. Sci. Phila., ser. 2, 6: 24, pl. 8, fig. 23; figured holotype ANSP 126522a. Lea, 1867, Obs. Unio, 11: 28. Simpson, 1914, Cat. Naiades, 1: 393.

Description. Shell medium to large, reaching over 165 mm in length. Outline subelliptical, more or less elongate. Valves of young specimens not much inflated, those of older ones quite inflated, thin, sometimes very thin. Anterior end regularly rounded; posterior end rather pointed. Ventral margin straight, or slightly curved, very occasionally slightly incurved. Dorsal margin slightly curved, often forming a winglike angle where it meets the obliquely descending posterior margin. The posterior margin joins the ventral margin in a broad point, somewhat below the medial line. Hinge ligament long and low. Posterior ridge indistinct. Posterior slope slightly concave, sometimes with two faint ridges. Umbos slightly swollen and moderately convex, located in the anterior third or fourth of the shell, their sculpture consisting of five to seven double-looped bars, not appreciably lower in front or behind the sinus, but of uniform elevation. Periostracum generally smooth and shiny, slightly roughened toward the margins and on the posterior slope. Surface of the shell sometimes uniformly straw yellow, but usually lighter to darker green with concentric lighter and darker bands, with darker rays on the disk. The rays on the posterior slope are darker, at least those rays on the faint ridges, though generally the whole posterior slope is blackish green.

No hinge plate or teeth; muscle scars inconspicuous and poorly defined. Nacre bluish white and iridescent.

Females are sometimes indicated by a swelling of the valves posterior to the middle, but this is not a uniform character.

Length mm	Height mm	Width mm	
165	86	62	Lake Michie, 12 mi. NNE Durham, Durham Co., North Carolina.
152	79	65	Savannah River, Johnsons Landing, 10 mi. W Allendale, Allendale Co., South Carolina (MZUM).
107	58	49	Swift Creek, near Macon [Bibb Co.], Georgia. Holotype of *A. dariensis* Lea.

Anatomy. Thoroughly discussed by Simpson (G. B., 1884) and commented upon by Reardon (1929: 8, pl. 3, figs. 1–10). The glochidia are hooked.

Breeding season. From August to May (Ortmann, 1919: 154).

Habitat. Lives in rivers and creeks in soft mud and sand; also in sand bars, generally in slowly moving water; prefers ponds.

Remarks. In the Atlantic Slope region *Anodonta cataracta* Say can be confused in the lower St. Lawrence drainage with *Anodonta cataracta fragilis* Lamarck (see Athearn and Clarke, 1962: 28; 1963: 22); *Anodonta implicata* Say under which see:

Remarks on p. 361; and in central New York with *Anodonta grandis* Say, of the Interior Basin. *A. cataracta* Say differs from *grandis* primarily in the umbonal sculpture, that of the latter consists of four to five bars of which the first two are concentric, while the others are distinctly double-looped, with a sharp re-entering sinus between the loops. The anterior loop is broadly rounded, the posterior loop is angular, narrow, and characteristically elevated into a tubercle. In *cataracta* the bars are of uniform height and are not tubercular. These distinctions were properly pointed out by Marshall (1890: 188, 189). Except for this minor difference the two species are very close, though *cataracta* tends to be a brighter green, and while short high examples of *cataracta* are found in rivers, these forms are more common in *grandis*. In general, *cataracta* is more elongated, especially individuals from ponds, and the posterior point is more elevated above the base line, rendering the ventral margin more convex. Ortmann (1919: 154) has clearly pointed out the different reaction of the two species to environment.

Specimens from the Alabama-Coosa River system show no morphological differences separating *hallenbeckii* (Lea) (Clench and Turner, 1956: 186) from *cataracta*. It is possible that *cataracta* arrived there through the commingling of the upper Alabama and Coosa rivers directly, though it is suggested elsewhere in this paper that *cataracta* may more likely have spread into the Apalachicola River system through a confluence of it with the Savannah, and then subsequently reached the Alabama system through a mingling of the waters of its Uphapee Creek and Uchee Creek of the Apalachicola River system. Most of the shells from Uphapee Creek are the long pond forms. I did not find any *Anodonta* in this broad, swift flowing creek in 1964, suggesting that the original lot was from a quiet backwater which I did not locate.

In the southern part of the Atlantic Slope *A. cataracta* is not very common. In the Altamaha River, at the stations listed below, only a few specimens were taken. Lea's specimen of *dariensis* from Hopeton, near Darien, McIntosh Co., Georgia, was not located, hence it is not included in the records since it might be *gibbosa*. In the Museum of Comparative Zoology there is a single specimen of *cataracta* from the C. B. Adams collection made before 1850, labeled Washington Co., Georgia. If this record is valid, then *cataracta* is found either in the upper Oconee River of the Altamaha River system or in the upper Ogeechee River system. This species becomes abundant and reaches large size in impounded waters, such as Lake Moultrie of the Cooper-Santee River system, South Carolina, Stewarts Mill Dam, Union Co., North Carolina, and Lake Michie on Flat River, North Carolina.

Range. Alabama-Coosa River system. Apalachicolan region: Choctawhatchee and upper Apalachicola River systems. Atlantic Slope: Altamaha River system, Georgia, north to the lower St. Lawrence River system, Canada. Interior Basin: probably extending from the St. Lawrence River system westward to Michigan.

Specimens Examined

Altamaha River System

Ocmulgee River Drainage. *Georgia:* Possum Lake, NE Stone Mountain, De Kalb Co. Swift Creek, near Macon, Bibb Co. Limestone Creek, near Hartford, Pulaski Co. (H. D. Athearn). Dicksons Creek, 10 mi. NE Fitzgerald, Ben Hill Co. Ocmulgee River, below Lumber City, Telfair Co. (H. D. Athearn).

Savannah River System

Savannah River Drainage. *South Carolina:* Savannah River, 6 mi. S Martin; Savannah River, Johnsons Landing, 10 mi. W Allendale; *both* (MZUM); *both* Allendale Co.

Cooper-Santee River System

Congaree River Drainage. *South Carolina:* Congaree River.

Catawba River Drainage. *North Carolina*: Bissels Pond, Charlotte, Mecklenburg Co. (USNM).

Wateree River Drainage. *South Carolina:* Wateree River, 2.5 mi. W Camden, Kershaw Co.

Santee River Drainage. *South Carolina:* Poplar Creek, Schulers Fish Pond, near Santee State Park; Eutaw Springs, [town of] Eutaw Springs; *both* Orangeburg Co. Lake Moultrie, Cross, Berkeley Co.

Pedee River System

Yadkin River Drainage. *North Carolina:* Salem, Forsyth Co. (USNM). Yadkin River, Rowan Co. Stewarts Mill Dam, Union Co. (USNM).

Waccamaw River System

Waccamaw River Drainage. *North Carolina:* Lake Waccamaw, [town of] Lake Waccamaw, Columbus Co.

Cape Fear River System

Cape Fear River Drainage. *North Carolina:* Travis Creek, 1.5 mi. N Gibsonville, Guilford Co. (MZUM). Rocky River, 11 mi. N Sanford, Chatham Co. Livingstons Creek [Brunswick Co.] (USNM).

Neuse River System

Neuse River Drainage. *North Carolina*: Lake Michie, 12 mi. NNE Durham Center, Durham Co. (75).

Roanoke River System

Dan River Drainage. *Virginia*: Aarons Creek, 3 mi. W Buffalo, Lithia Springs; Dan River; *both* Halifax Co.

Roanoke River Drainage. *North Carolina*: Roanoke River, Weldon, Halifax Co. (USNM).

James River System

James River Drainage. *Virginia*: Calfpasture River (Conrad, 1846: 407).

Rappahannock River System

Rapidan River Drainage. *Virginia*: Mountain Run, Orange Co. (MZUM).

Potomac River System

Potomac River Drainage. *Pennsylvania:* Great Tonoloway Creek, Thompson Township, Fulton Co. (Ortmann, 1919: 156). Conococheague Creek, Greencastle, Franklin Co. (Ortmann, 1919: 156). *West Virginia:* South Branch, Potomac River, Romney, Hampshire Co. (Ortmann, 1919: 157). *Virginia:* South River (upper Shenandoah River), Waynesboro, Augusta Co. (Ortmann, 1919: 157). Potomac River, Great Falls Co. Park, Fairfax Co. *District of Columbia:* Aqueduct Lake.

Anodonta (Pyganodon) gibbosa Say
Plate 15: 2, 3

Anodonta gibbosa Say 1824 *in* W. H. Keating, Narrative of an Expedition to the Source of the St. Peters River, 2: 265, pl. 14, figs. 3–4 (South Carolina; type, ANSP [lost]. Type locality is here restricted to Altamaha River, Hopeton, near Darien, McIntosh Co., Georgia. See: *Remarks* below). Simpson, 1914, Cat. Naiades, 1: 397.

Anodonta gibbosa Say, *partim*. Clench and Turner, 1956, Bull. Florida State Mus., 1: 184.

Description. Shell medium to large, reaching 120 mm in length. Outline subelliptical. Valves very much inflated, thin and smooth. Anterior end regularly rounded; posterior end broadly rounded or somewhat pointed. Ventral margin usually broadly curved, though centrally sometimes straight, or slightly incurved. Dorsal margin slightly curved, usually forming a distinct winglike angle where it meets the obliquely descending posterior margin. The posterior margin joins the ventral margin in a broad point near the medial line. Hinge ligament long and low. Posterior ridge broadly rounded, though occasionally with a trace of an angle. Posterior slope slightly concave. Umbos very high and broad, located in the anterior third of the shell, their sculpture consisting of a number of low double-looped ridges. Perios-

tracum generally smooth and shiny, slightly roughened toward the margins and on the posterior slope. Surface of the shell straw yellow to greenish, older specimens becoming chestnut to blackish. Usually with very fine greenish rays; the several on the posterior slope usually darker and broader than those on the disk.

No hinge plate or teeth; muscle scars inconspicuous and poorly defined. Nacre bluish white and iridescent, sometimes pinkish toward the umbonal cavities.

Length mm	Height mm	Width mm	
123	72	69	Altamaha River, 3 mi. NW Everett City, Glynn Co., Georgia.
97	59	48	Cedar Creek, Fountains Mill, 7 mi. SW Hawkinsville, Pulaski Co., Georgia.
74	49	40	[after Say].
71	47	37	Altamaha River, Hopeton, near Darien, McIntosh Co., Georgia.

Habitat. Lives in soft mud and sand, also in sand bars; generally in slowly moving water.

Remarks. In the Atlantic Slope region, *Anodonta gibbosa* Say can only be confused with *A. cataracta* Say, but *gibbosa* has a very swollen shell, the umbos are greatly protruded, and the swelling continues with the growth of the shell, the greatest swelling extending toward the posterior ventral margin. Frierson (1912: 129) correctly pointed out the relationship of this species to *A. cataracta* Say based on the beak sculpture, but thought *gibbosa* might be merely a subspecies. They appear to be separate and both species occur in the Altamaha River system.

It is obvious that Major Le Conte who sent T. Say the type of *gibbosa* made a mistake as to its locality, since there are no specimens of this species in any of the collections studied from South Carolina. Le Conte was to later send I. Lea numerous species he collected in the lower Altamaha River, so it is presumed that this species was also from this region, especially since a specimen in the Museum of Comparative Zoology from B. Walker, collected at Hopeton on the lower Altamaha, has almost the same measurements as the type. To avoid confusion the restriction of the type locality to this region seems warranted.

Clench and Turner (1956: 185) included under this name the *Anodonta* of the Ochlockonee, Apalachicola and Choctawhatchee River systems, but these *Anodonta* are more elliptical and elongate, much less globose, and with the more tuberculous beak sculpture of *Anodonta grandis* Say, which they appear to be.

Range. Southern Atlantic Slope: restricted to the Altamaha River system, Georgia.

Specimens Examined

Altamaha River System

Ocmulgee River Drainage. *Georgia*: Cedar Creek, Fountains Mill, 7 mi. SW Hawkinsville, Pulaski Co. Ocmulgee River, 1 mi. S Lumber City, Telfair Co.

Altamaha River Drainage. *Georgia*: Altamaha River, 10 mi. NE Surrency, Appling Co. Altamaha River, "Riverside Park," 4 mi. N Jesup, Wayne Co. Altamaha River, 3 mi. NW Everett City, Glynn Co. Buttonwood Swamp, Liberty [now Long] Co. Altamaha River, Hopeton, near Darien, McIntosh Co.

Anodonta (*Pyganodon*) *implicata* Say

Plate 15: 4
Plate 16: 1, 2

Anodonta implicata Say 1829, New Harmony [Indiana] Disseminator 2, no. 22, p. 340 (pond in Danvers [Essex Co.], Massachusetts; type, ANSP [lost]).

The type locality was changed to Agawam River (outlet of Halfway Pond), Plymouth [Plymouth Co.], Massachusetts, and a neotype MCZ 176769 was selected by Johnson, 1946, Occ. Papers on Moll., 1: 112, pl. 16, figs. 1, 2). Simpson, 1914, Cat. Naiades, 1: 391. Ortmann, 1919, Mem. Carnegie Mus., 8: 159, pl. 11, figs. 2, 3. Clarke and Berg, 1959, Cornell Univ. Exp. Sta. Mem., no. 367, p. 40, fig. 42. Athearn and Clarke, 1962, Natl. Mus. Canada, Bull. no. 183, p. 26, pl. 2, figs. 1, 2.

Anodonta newtonensis Lea 1838, Trans. Amer. Philos. Soc., 6: 79, pl. 21, fig. 66 (Newtown [Newton] Creek, [Camden Co., New Jersey], opposite Philadelphia; figured type not in USNM or ANSP [lost]; Schuylkill [River], Fairmount [Philadelphia, Philadelphia Co., Pennsylvania], lectotype USNM 86561 selected by Johnson, 1946, Occ. Papers on Moll., 1: 112. [The selection of lectotypes, without figuring them, is a dubious contribution to knowledge, if, indeed, such selections are valid at all.] Figured here, Pl. 15: 4. Lea, 1838, Obs. Unio, 2: 79.

Anodonta housatonica Linsley 1845, Amer. Jour. Sci., ser. 1, 48: 277 (Housatonic [River], Corum [near Huntington, Fairfield Co.], Connecticut), [*nomen nudum*]. Gould, 1848, Amer. Jour. Sci., ser. 2, 6: 234, figs. 4, 5; measured and figured holotype USNM 678302.

Description. Shell medium to large, reaching 165 mm in length. Outline elongate-elliptical to elongate-ovate. Valves quite inflated, somewhat subcylindrical, rather solid and heavy for an *Anodonta*. Anterior end regularly rounded; posterior end more acutely rounded, older specimens often becoming subtruncated. Ventral margin slightly rounded, becoming straight or slightly arcuate in old individuals. Dorsal margin straight, occasionally forming a slight winglike angle where it meets the obliquely descending posterior margin. Hinge ligament long and low. Posterior ridge not very acute, but generally distinctly biangulate. Posterior slope slightly concave. Umbos slightly swollen and moderately convex, located in the anterior third of the shell, their sculpture consisting of five to seven double-looped bars, not appreciably lower in front or behind the sinus but of uniform elevation. Periostracum generally rather smooth, save for growth lines and occasional plaiting, yellowish brown or greenish brown, sometimes becoming reddish brown or almost black in old specimens. Immatures are sometimes greenish and obscurely rayed.

No hinge plate or teeth. Beak cavities rather shallow. Muscle scars and pallial line distinct especially in mature specimens. Shell distinctly thickened along the anterior margin below the pallial line. Nacre dull opalescent, generally pale copper, pinkish, or, more rarely, white or bluish white, sometimes with a bluish cast toward the margins.

Females are usually more swollen than males in the middle portion of the disk, which tends to make the lower margin more curved and the shell somewhat shorter and higher than that of the male, but this is not a uniform character.

Length mm	Height mm	Width mm	
162	77	66	Agawam River, Plymouth, Plymouth Co., Massachusetts. Male.
120	60	48	As above. Neotype of *A. implicata* Say. Male.
97	52	39	Schuylkill River, Fairmount, Philadelphia Co., Pennsylvania. Lectotype of *A. newtonensis* Lea. Female.
94	51	34	Housatonic River, Corum, Fairfield Co., Connecticut. Holotype of *A. housatonica* Gould. Male.

Anatomy. The anatomy of this species has not been investigated. The glochidia are rather large, subtriangular, with a spine at the tip of each valve. The host fish is the alewife, *Alosa pseudoharengus* (Wilson) (Johnson, 1946: 112).

Breeding season. According to Ortmann (1911: 303) all *Anodonta* are bradytictic, or winter breeders, the marsupia filling sometime in summer between July and September. The glochidia are carried through the winter and set free when warmer weather begins. I collected gravid females at Plymouth, Massachusetts, on May 8, 1943, and June 9, 1946.

Habitat. Lives in sand or gravel, rarely in mud. Found abundantly, close to the coast in ponds that have an unobstructed outlet to the ocean. Seems to prefer a stream environment; the largest examples have been taken in a relatively swift, sandy stream.

Remarks. Anodonta implicata Say of the

Northern Atlantic Slope can generally be easily separated from all other species of *Anodonta*. The most reliable and constant feature in identifying adults of this species is the pronounced thickening of the anterior-ventral portion of the shell below the pallial line. This thickening is not always pronounced in immatures, but may still be detected. Other characteristics of this species are the dark and usually yellowish or brownish rayless periostracum and the pale copper or salmon color of the nacre.

Anodonta implicata is especially abundant in the region of Cape Cod, Massachusetts, where it reaches its greatest size. The tide waters of the Potomac River, Virginia, seem to be its southern terminus. All the specimens under this name I have seen from rivers below the Potomac were heavy *cataracta*, which have an especially distinct pallial line anteriorly, but which lack the special anterior-ventral thickening of the shell and the characteristic nacre color. It is on the basis of such specimens that Athearn and Clarke (1962: 26) suggest that this species extends to South Carolina.

Range. Northern Atlantic Slope: Potomac River, Maryland, north to New Brunswick and northern Nova Scotia, *both* Canada.

Specimens Examined

Potomac River System

Potomac River Drainage. *District of Columbia:* Potomac River (USNM).

Subgenus *Utterbackia* F. C. Baker

Utterbackia F. C. Baker 1927, American Midland Nat., 10: 221, 222 (misspelled as *Utterbachia* on p. 221).

Type species, *Anodonta imbecillis* [*sic*] Say. Original designation.

Utterbackiana Frierson 1927, Check List North American Naiades, p. 17.

Type species, *Anodonta suborbiculata* Say. Monotypic.

Under the subgenus *Lastena* Rafinesque (not available for use here since the type is *Anodonta lata* Rafinesque, *teste* Ortmann and Walker, 1922: 32), Frierson included all of the taxa mentioned in the present paper, except *A. suborbiculata* Say of the Interior Basin for which he introduced the subgeneric name *Utterbackiana*, on the basis that that species is dioecious. But, as mentioned below, this as an unreliable basis for classification and the shell morphology is clearly that of *Utterbackia*.

Morrison (*in* Walter, 1956: 265) states that *Anodonta imbecilis*, like *A. cygnea* of Europe and Asia, is monoecious and has flat umbos, and that therefore *imbecilis* belongs to *Anodonta s. s.*

Heard (1966: 31) has clearly shown that sexuality is an unreliable means of classifying *Anodonta*. Neither *cygnaea* nor *imbecilis* are uniformly monoecious. The flat umbos of *Utterbackia* and *Anodonta s. s.* appear to be a convergent character. *Utterbackia* is quite isolated from *Anodonta s. s.* in North America, the latter being restricted to the Pacific region. All four species of *Utterbackia* are more delicate than *cygnea*, and some individuals of each of the species exhibit fine rays toward the umbos. These are lacking in *cygnea* or any other *Anodonta*.

There are two species of *Utterbackia* in the Interior Basin, *suborbiculata* and *imbecilis*. The latter is found almost everywhere to the east except Peninsular Florida and the Northern Atlantic Slope region. Speciation has taken place in the Southeastern states, where two species, in addition to *imbecilis*, occur. They are *couperiana* Lea, covered here, and *A. peggyae* Johnson (1965), which occurs in the Apalachicolan region and Gulf drainage of Peninsular Florida.

Anodonta (*Utterbackia*) *imbecilis* Say
Plate 16: 3

Anodonta (*Lastena*) *ohiensis* Rafinesque 1820, Ann. Gén. Sci. Physiques (Bruxelles), 5: 316 (l'Ohio et toutes les rivières adjacentes; supposed type, ANSP 216908, is *Proptera laevissima* (Lea)). Ortmann and Walker (1922, Occ. Papers, Mus. Zool. Univ. Michigan, no. 112, p.

37) clearly showed that *A. ohiensis* is not identifiable, nevertheless Frierson (1927, Check List North American Naiades, p. 18) persisted in using this name for *A. imbecilis* Say.

Anodonta imbecilis Say 1829, New Harmony [Indiana] Disseminator, 2(23): 355. (Wabash River, Indiana; type, ANSP [lost]). Neotype Senckenberg Mus. 4301 [not seen] selected, but not figured, by Haas, 1930, Senckenbergiana, 12: 326. Type locality restricted to Wabash River, New Harmony, Indiana, by Clench and Turner, 1956, Bull. Florida State Mus., 1: 188.

Anodonta incerta Lea 1834, Trans. Amer. Philos. Soc., 5: 56, pl. 6, fig. 16 (Ohio River, near Cincinnati [Hamilton Co., Ohio]; type, not in USNM or ANSP [lost]. Lea, 1834, Obs. Unio, 1: 158.

Anodon horda Gould 1855, Proc. Boston Soc. Nat. Hist., 5: 229 (Comanche Creek [Tributary of The Llano River, close to the present site of Mason, Mason Co.], Texas [*teste*, Taylor, 1967, Veliger, 10: 153]; measured holotype USNM 678301).

Anodonta henryana Lea 1857, Proc. Acad. Nat. Sci. Phila., 9: 102 (Matamoras, Tamaulipas [State], Mexico). Lea, 1860, Jour. Acad. Nat. Sci. Phila., ser. 2, 4: 373, pl. 66, fig. 198; figured holotype USNM 86692. Lea, 1860, Obs. Unio, 8: 55.

Utterbackia imbecillis [*sic*] *fusca* Baker 1927, American Midland Nat., 10: 222 (Sturgeon Bay, Door Co., Wisconsin; holotype MZUM 209141, figured by Baker, 1928, Bull. Wisconsin Geol. Nat. Hist. Survey, no. 70(2): 175, pl. 103, fig. 14).

Anodonta imbecillis [*sic*] Say. Simpson, 1914, Cat. Naiades, 1: 396.

Anodonta henryana Lea. Simpson, 1914, Cat. Naiades, 1: 396.

Anodonta ohiensis Rafinesque. Ortmann, 1919, Mem. Carnegie Mus., 8: 162.

Anodonta imbecilis Say, *partim*. Clench and Turner, 1956, Bull. Florida State Mus., 1: p. 187. See: Johnson, 1965, Breviora, Mus. Comp. Zool., no. 213, pl. 2, fig. 5, 6.

Anodonta (*Utterbackia*) *imbecilis* Say. Clarke and Berg, 1959, Cornell Univ. Exp. Sta. Mem. no. 367, p. 40, fig. 42.

Description. Shell small to medium, usually not reaching over 90 mm in length. Outline rather elongated, subelliptical. Valves compressed, or only slightly swollen in young shells, but often becoming quite inflated with age, very thin, fragile, and smooth. Anterior end regularly rounded; posterior end somewhat pointed. Ventral margin slightly convex, often almost straight in the middle. Dorsal margin straight and long, usually forming a distinct angle where it meets the obliquely descending posterior margin. The posterior margin joins the curved ventral margin in a point near the medial line. Hinge ligament short and inconspicuous. Posterior ridge broadly rounded, though occasionally rather angular. Posterior slope slightly concave. Umbos low and broad, seldom extending above the dorsal margin, located in the anterior third of the shell, their sculpture consisting of a number of delicate subconcentric undulations. Periostracum smooth and shiny, except the posterior slope which may be slightly roughened. Surface of the shell straw yellow to greenish yellow, but more generally darker green, sometimes grass green. Toward the umbos the color may be greyish, brownish or yellowish, with concentric darker growth-rests. The disk may be obscurely rayed; the posterior slope usually has two or three dark green to blackish rays.

No hinge plate or teeth; muscle scars inconspicuous and poorly defined. Nacre bluish white and iridescent, sometimes pinkish toward the umbonal cavities.

This species is hermaphroditic and does not show any sexual differences.

Length mm	Height mm	Width mm	
90	42	34	Magnolia Springs, Magnolia State Park, Perkins, Jenkins Co., Georgia.
84	44	31	Outlet of Waynesboro Lake, Waynesboro, Burke Co., Georgia.
71	39	24	Buck Creek, 5 mi. NW Hawkinsville, Pulaski Co., Georgia.

Anatomy. Clarke (1959: 42) discusses the work that has been done on the anatomy of this species. He suggests that the host fish is *Semotilus atromaculatus atromaculatus* (Mitchill).

Breeding season. Ortmann (1919: 163) says this species is undoubtedly bradytictic.

Habitat. Lives in soft mud or sand in ponds, creeks, and near the banks of larger rivers.

Remarks. In the Atlantic Slope region, *Anodonta imbecilis* Say can only be confused with *A. couperiana* Lea and in the Apalachicolan region it can only be mistaken for *Anodonta peggyae* Johnson. These three species of *Anodonta* are the only ones in these drainage systems whose umbos do not extend above the dorsal margin. In *imbecilis* the ventral margin is almost parallel to the dorsal one, while in *couperiana* the ventral margin is broadly curved, which renders the shell much higher in proportion to its length than *imbecilis*. See: *Remarks* under *Anodonta couperiana* Lea on p. 365.

The general distribution of *A. imbecilis* has been discussed by Ortmann (1919: 165). It is found in the Apalachicolan region east to the Ochlockonee River system, Florida. In the Atlantic Slope region it does not extend below the Altamaha River system, Georgia. It apparently does not occur in Peninsular Florida, since the author made an extensive collecting trip to this area in 1962 and did not find *A. imbecilis*. It is replaced on the Gulf side of Florida by *Anodonta peggyae* Johnson (1965: 1) and by *A. couperiana* Lea on the Atlantic side. (See: Johnson, 1965, pl. 1.) On the Atlantic slope, *A. imbecilis* extends to the Nottoway River, Virginia, of the Chowan River system. Ortmann (1919: 163) records this species from Pennsylvania in the region of Lake Erie, but not from the Atlantic Slope. It has since been found at Gunpowder River, Loch Raven Dam, Loch Raven, Baltimore Co., Maryland (ANSP).

Range. Interior Basin: Mississippi drainage generally, Ohio River, West Gulf Coastal region, Alabama-Coosa River system; and Apalachicolan region: Rio Grande River system, Texas, east to the Ochlockonee River system, Florida. Southern Atlantic Slope: Altamaha River system, Georgia, north to the Chowan River system. Northern Atlantic Slope: Gunpowder River system, Maryland.

Specimens Examined

Altamaha River System

Ocmulgee River Drainage. *Georgia*: Buck Creek, 5 mi. NW Hawkinsville; Cedar Creek, Fountains Mill, 7 mi. WSW Hawkinsville; *both* Pulaski Co.

Ohoopee River Drainage. *Georgia*: Yam Grande Creek, 3 mi. W Swainsboro, Emanuel Co.

Altamaha River Drainage. *Georgia*: Altamaha River, 4 mi. NE Jesup, Wayne Co.

Ogeechee River System

Ogeechee River Drainage. *Georgia*: Magnolia Springs, Perkins, Jenkins Co. Mill Creek, 5 mi. E Midville; Barkcamp Creek, 7 mi. E Midville; *both* Burke Co.

Savannah River System

Savannah River Drainage. *Georgia*: Savannah River, 7.5 mi. NE Shellbluff; outlet of Waynesboro Lake, Waynesboro; Savannah River, 6 mi. NE Girard; *all* Burke Co. *South Carolina:* Savannah River, 6 mi. S Martin; Savannah River, Johnsons Landing, 10 mi. W Allendale; Savannah River, Kingjaw Point, 10 mi. WSW Allendale (ANSP); *all* Allendale Co.

Cooper-Santee River System

Catawba River Drainage. *North Carolina*: Bissels Pond, Charlotte, Mecklenburg Co. (ANSP; USNM).

Wateree River Drainage. *South Carolina:* Wateree River, 2.5 mi. W Camden, Kershaw Co.

Santee River Drainage. *South Carolina*: Santee River, above dam, near Cross; Charleston (USNM); *both* Berkeley Co.

Pedee River System

Yadkin River Drainage. *North Carolina:* Salem, Forsyth Co. (USNM).

Cape Fear River System

Cape Fear River Drainage. *North Carolina:* Greenfield Mill Pond, Wilmington, New Hanover Co. (Ortmann, 1919: 164).

Chowan River System

Nottoway River Drainage. *Virginia:* Birchen Lake, on Birchen Creek, Camp Pickett, Nottoway Co.

Gunpowder River System

Gunpowder River Drainage. *Maryland:* Gunpowder River, Loch Raven Dam, Loch Raven, Baltimore Co. (ANSP).

Anodonta (Utterbackia) couperiana Lea

Plate 16: 4
Plate 17: 1

Anodonta cowperiana [*sic*] Lea 1840, Proc. Amer. Philos. Soc., 1: 289 (Hopeton, near Darien [McIntosh Co.], Georgia). Changed to:

Anodonta couperiana Lea 1842, Trans. Amer. Philos. Soc., 8: 227, pl. 20, fig. 46; figured type, not in USNM [lost]. Lectotype, USNM 86673, selected by Johnson, 1965, Breviora, Mus. Comp. Zool., no. 213, p. 3, pl. 2, fig. 4. Lea, 1842, Obs. Unio, 3: 65.

Anodonta dunlapiana Lea 1842, Proc. Amer. Philos. Soc., 2: 225 (South Carolina). Lea, 1842, Trans. Amer. Philos. Soc., 8: 248, pl. 27, fig. 65; figured type, not in USNM [lost]. Lectotype, here selected, USNM 86564, Pl. 17, fig. 1, [Charleston, Chatham Co.] South Carolina. Lea, 1842, Obs. Unio, 3: 86.

Anodonta cowperiana [*sic*] Lea. Clench and Turner, 1956, Bull. Florida State Mus., 1: 183, pl. 6, fig. 3.

Description. Shell medium to large, reaching 110 mm in length. Outline subelliptical to subcircular. Valves somewhat inflated, thin, fragile, and smooth. Anterior end regularly rounded; posterior end somewhat pointed. Ventral margin broadly curved. Dorsal margin straight and long, usually forming a distinct winglike angle where it meets the obliquely descending posterior margin. Hinge ligament short but prominent. The posterior margin joins the curved ventral margin in a point near the medial line. Posterior ridge broadly rounded. Posterior slope slightly concave. Umbos low and broad, seldom extending above the dorsal margin, located in the anterior third of the shell, their sculpture consisting of a number of delicate subconcentric undulations. Periostracum smooth and shiny, except the posterior slope which may be roughened. Surface of the shell straw yellow to yellowish green, usually with numerous and generally fine green rays, sometimes with distinctly darker rays on the posterior slope.

No hinge plate or teeth; muscle scars inconspicuous and poorly defined. Nacre bluish white and iridescent.

Length mm	Height mm	Width mm	
110	67	49	Sandpit, near Edisto River, Givhans Ferry State Park, 2 mi. NW Givhans, Dorchester Co., South Carolina.
87	50	35	Pond, near Savannah, Chatham Co., Georgia.
83	46	35	Charleston, South Carolina. Lectotype of *A. dunlapiana* Lea.
67	38	29	Hopeton, near Darien, McIntosh Co., Georgia. Lectotype of *A. couperiana* Lea.

Anatomy. Discussed by Lea (1863: 451).

Habitat. Prefers sandy or muddy bottoms of ponds and sluggish streams.

Remarks. In the Southern Atlantic Slope region, *Anodonta couperiana* Lea can be confused only with *A. imbecilis* Say. Both species have umbos which do not extend above the dorsal margin, a character which distinguishes them from the other *Anodonta* of the Atlantic Slope. *A. couperiana* is differentiated from *imbecilis* by its green rays, which are especially fine on the disk, and by its broadly curved ventral margin, which renders the shell much higher in proportion to its length than *imbecilis*, whose ventral margin is almost straight and parallel to the dorsal one. The height/length ratio of *couperiana* is about 2 to that of 1.5 in *imbecilis*.

A. couperiana is found in the Apalach-

icola River system with *A. peggyae* Johnson, which differs from *couperiana* by being subrhomboidal rather than elliptical in outline, and by being more biangulate posteriorly, with the biangulation ending near the base. *A. couperiana* is more pointed posteriorly with the point ending near the medial line. In *A. peggyae*, when the dorsal margin is held straight, the ventral margin is often obliquely descending toward the broad posterior basal biangulation.

A. couperiana is a rare species in Georgia, but the specimens from the northern part of the range are remarkable for their size and beauty. It is common and abundant in Central Florida, where individuals tend to be small.

Range. Apalachicolan region: Apalachicola, Ochlockonee, and St. Marys river systems. Peninsular Florida. Southern Atlantic Slope: Altamaha River system, Georgia, north to the Cape Fear River system, North Carolina.

Specimens Examined

Saint Marys River System

Saint Marys River Drainage. *Florida*: St. Marys River (ANSP; MZUM).

Altamaha River System

Altamaha River Drainage. *Georgia*: Rice field ditches on the Altamaha River, Hopeton, near Darien, McIntosh Co.

Savannah River System

Savannah River Drainage. *South Carolina:* Brickyard Pond, Hamburg, Aiken Co. (USNM). Savannah River [Johnsons Landing], 10 mi. W Allendale; Savannah River, Kingjaw Point, 10 mi. WSW Allendale (ANSP); *both* Allendale Co. *Georgia:* Pond near Savannah, Chatham Co.

Combahee River System

Salkehatchie River Drainage. *South Carolina:* Pauline Cave, near Kline, Barnwell Co. (ANSP).

Edisto River System

Edisto River Drainage. *South Carolina:* Sandpit, near Edisto River, Givhans Ferry State Park, 2 mi. NW Givhans, Dorchester Co. Charleston, Chatham Co. (USNM).

Cooper-Santee River System

Saluda River Drainage. *South Carolina*: Milton, Laurens Co.

Cape Fear River System

Cape Fear River Drainage. *North Carolina:* Greenfield Mill Pond, Wilmington, New Hanover Co. (USNM).

Genus *Strophitus* Rafinesque

Strophitus Rafinesque 1820, Ann. Gén. des Sci. Physiques (Bruxelles), 5: 316.

Type species, *Anodonta undulata* Say. Monotypic. Ortmann, 1912, Ann. Carnegie Mus., 8: 299.

Pseudodontoideus Frierson 1927, Check List North American Naiades, p. 9, 23. Instituted as a subgenus.

Type species, *Margaritana alabamensis* Lea. Original designation.

Strophitus contains two species, *undulatus* (Say), which is widely distributed throughout the Interior Basin and Atlantic Slope region, and *subvexus* (Conrad) (Johnson, 1967: 3, pl. 1, figs. 1–3), which extends from the eastern part of the West Gulf Coastal region through the Apalachicolan region. All of the taxa included by Frierson under *Strophitus s. s.* and *Pseudodontoideus* Frierson are included in the synonymy of the two species mentioned above, except for: *Strophitus undulatus tennesseensis* Frierson, which may be a geographic subspecies in the modern sense; and *Strophitus radiatus* (Conrad), which belongs under *Anodontoides radiatus* (Conrad) (Johnson, 1967: 6, pl. 2, figs. 1–4).

Generally, Frierson gave neither descriptions nor reasons for instituting new subgenera, but it is presumably on the basis of the vestigial pseudocardinal teeth found in *alabamensis* (= *subvexus*) that

he instigated *Pseudodontoideus* as a subgenus. If the present synonymy of the species is correct, *Strophitus* does not need subdivision.

Strophitus undulatus (Say)
Plate 17: 2, 3

Anodonta undulata Say 1817, Nicholson's Encyclopedia, 2 [no pagination], pl. 3, fig. 6 (no type locality, here restricted: Schuylkill River, near Philadelphia, Philadelphia Co., Pennsylvania; type, ANSP [lost]).

Anodonta pensylvanica [*sic*] Lamarck 1819, Hist. Nat. des Animaux sans Vertèbres, 6: 86 (la rivière de Schuglkill [Schuylkill], près de Philadelphie [Philadelphia Co., Pennsylvania]; holotype, Geneva Museum, figured by Delessert, 1841, Rec. Coquilles de Lamarck, pl. 13, figs. 4a, 4b).

Anodon rugosus Swainson 1822, Zool. Illustrations, ser. 1, 2, pl. 96 (United States; type [location unknown]).

Anodon areolatus Swainson 1829, Zool. Illustrations, ser. 2, 1, pl. 18 (North America; type [location unknown]).

Alasmondonta edentula Say 1829, New Harmony [Indiana] Disseminator 2, no. 22, p. 340 (Wabash River [near New Harmony, Posey Co., Indiana]; type, ANSP [lost]).

Anodonta virgata Conrad 1836, Monography Unionidae, no. 5, back cover (Buck Creek, Clarke Co., Ohio; type ANSP [lost]).

Anodonta pavonia Lea 1836, Trans. Amer. Philos. Soc., 6: 78, pl. 21, fig. 65 (headwaters of the Little Beaver [River, Lawrence Co.], Ohio; figured holotype USNM 86514). Lea, 1838, Obs. Unio, 2: 78.

Anodonta wardiana Lea 1838, Trans. Amer. Philos. Soc., 6: 46, pl. 14, fig. 42 ([Scioto River], near Chillicothe [Ross Co.], Ohio; figured holotype USNM 86488). Lea, 1838, Obs. Unio, 2: 46.

Anodon unadilla De Kay 1843, Zool. New York, Moll., pt. 5: 199, pl. 15, fig. 228 (Unadilla River, a tributary of the Susquehanna [River system], Otsego Co., New York; type, New York Lyceum of Nat. Hist. [destroyed by fire]).

Anodonta tetragona Lea 1845, Proc. Amer. Philos. Soc., 4: 165 (Alexandria [Rapides Parish], Louisiana). Lea, 1848, Trans. Amer. Philos. Soc., 10: 82, pl. 8, fig. 25; figured holotype USNM 86682. Lea, 1848, Obs. Unio, 4: 56.

Anodonta arkansensis Lea 1852, Trans. Amer. Philos. Soc., 10: 293, pl. 29, fig. 56 (Little Arkansas River, where the road to Santa Fé crosses it [Sedgwick Co., Kansas]; figured holotype USNM 86603). Lea, 1852, Obs. Unio, 5: 49.

Anodonta shaefferiana Lea 1852, Trans. Amer. Philos. Soc., 10: 288, pl. 26, fig. 50 (Horn Lake Creek [Shelby Co.], Tennessee; figured holotype USNM 86685). Lea, 1852, Obs. Unio, 5: 44.

Alasmodon rhombica Anthony 1865, Amer. Jour. Conch., 1: 158, pl. 12, fig. 5 (Michigan; figured holotype MCZ 50296).

Anodon papyracea Anthony 1865, Amer. Jour. Conch., 1: 161, pl. 15, fig. 2 (locality unknown [Potomac River, Virginia]; figured holotype MCZ 150656).

Anodon annulatus Sowerby 1867, Conch. Iconica, 17, *Anodon*, pl. 18, fig. 67 (Hab. ?; Cuming collection in BMNH [lost]).

Anodon quadriplicatus Sowerby 1867, Conch. Iconica 17, *Anodon*, pl. 28, fig. 110 (Potomac River, [Virginia]; holotype in Walpole coll., not in BMNH, [probably lost]).

Anodonta salmonia Clessin 1873, Conch. Cab., ser. 2, 9, pt. 1: 91, pl. 24, figs. 1, 2 (Nordamerika, im Ohio-und Wabash-Fluss); *non* Lea 1838.

Strophitus undulatus ovatus Frierson 1927, Check List North American Naiades, p. 22 (Middle West [Lyon Creek, Edwards Co., Illinois]; syntype MZUM 87584).

Strophitus rugosus pepinensis Baker 1928, Bull. Wisconsin Geol. Nat. Hist. Survey, no. 70(2), p. 204, pl. 74, fig. 8 (Lake Pepin near Lake City [Wabasha Co.], Minnesota; holotype MZUM 209137).

Strophitus rugosus winnebagoensis Baker 1928, Bull. Wisconsin Geol. Nat. Hist. Survey, no. 70(2), p. 205, pl. 74, figs. 1–6 (Lake Winnebago, Long Point Island, Wisconsin; holotype MZUM [original no. Univ. of Wisconsin 943a]).

Strophitus rugosus lacustris Baker 1928, Bull. Wisconsin Geol. Nat. Hist. Survey, no. 70(2), p. 207, pl. 75, figs. 6–8 (Oconomowoc Lake, Waukesha Co., Wisconsin; holotype Univ. Illinois, Urbana Z-22073 [not seen]).

Strophitus edentulus (Say). Simpson, 1914, Cat. Naiades, 1: 345. Ortmann, 1919, Mem. Carnegie Mus., 8: 197, pl. 12, figs. 7, 8.

Strophitus undulatus (Say). Simpson, 1914, Cat. Naiades, 1: 349. Ortmann, 1919, Mem. Carnegie Mus., 8: 195, pl. 12, fig. 6. Clarke and Berg, 1959, Cornell Univ. Exp. Sta. Mem., no. 367, p. 43, fig. 41. Athearn and Clarke, 1962, Natl. Mus. Canada, Bull. no. 183, p. 29, pl. 3, figs. 7, 8.

Description. Shell medium, seldom exceeding 90 mm in length in the Atlantic boid to subrhomboid. Valves subinflated, generally rather thin, inequilateral. Anterior end regularly rounded; posterior end more broadly rounded, somewhat pointed

or subtruncated. Ventral margin slightly curved, occasionally incurved. Dorsal mardrainage. Outline subelliptical, long rhomgin straight, ending in a slight angle with the obliquely descending posterior margin. Hinge ligament not very prominent. Posterior ridge very rounded, but occasionally slightly angular with a trace of a secondary ridge above, ending in a slight biangulation near the base. Umbos rather full, located in the anterior third of the shell, their sculpture consisting of a few very strong ridges which turn up posteriorly where there are a few radial lirae. Surface of the shell with fine irregular growth lines, generally smooth and shiny, though sometimes covered with brownish periostracum. When not heavily covered with periostracum, the shell may be yellowish, greenish or tawny, often with greenish rays over the entire surface or on the posterior slope.

Each valve has vestiges of pseudocardinal teeth which are merely slight swellings, anterior to the umbos. The hinge plate is narrow, and slightly incurved in front of the umbos. Lateral teeth are absent. Beak cavities shallow, with muscle scars on the hinge plate; anterior adductor muscle scars distinct, posterior ones faint. Pallial line scarcely visible. Nacre bluish, straw-colored or pinkish toward the umbos.

Length mm	Height mm	Width mm	
88	55	24	Swift Creek, 3 mi. SSW Garner, Wake Co., North Carolina.
74	44	27	Turkey Creek, 8 mi. NW Edgefield, Edgefield Co., South Carolina.
47	29	17	As above.

Anatomy. Figured by Lea (1838, pl. 15, fig. 47). Discussed by Ortmann (1911: 299). The glochidia are subtriangular, with hooks, and measure 0.36 mm in length and 0.30 mm in height. They may either complete their development in the marsupia of the parent or metamorphose while parasitizing the largemouth bass, *Micropterus salmoides* (Lacépède), or northern creek chub, *Semotilus atromaculatus* (Mitchill) (Baker, 1928: 201); both extend over the entire range of *S. undulatus* (Say).

Breeding season. From July to April or May of the following year.

Habitat. Lives in small rivers and creeks in mud, sand or gravel.

Remarks. Strophitus undulatus (Say), is the only species of *Strophitus* in the Interior Basin and Atlantic Slope region. The shell has no striking characters and might be confused with species of *Anodonta*, since members of both genera lack lateral teeth. *Anodonta* have no pseudocardinals, and do have a straight hinge line; whereas *Strophitus* have vestigial pseudocardinals which appear as slight swellings anterior to the umbos, and a hinge line which is incurved in front of the umbos.

S. undulatus is replaced in the Alabama-Coosa River system and Apalachicolan region by *S. subvexus* (Conrad) (Johnson, 1967: 2) which differs from *undulatus* by being distinctly rhomboidal, having a sharper posterior ridge, and by having at least one pseudocardinal in each valve elevated slightly above the hinge line.

Strophitus undulatus might be confused with *Anodontoides radiatus* (Conrad) (Johnson, 1967: 6) in these areas, except that *radiatus* is more elliptical, has broad green rays, and each valve has a long, narrow pseudocardinal tooth which is slightly elevated and roughly parallel to the hinge line.

Clarke and Berg (1959: 43) have already discussed the necessity of discarding the name *rugosus* Swainson for this species. Ortmann (1919: 195) stated that *undulatus* was only a poorly defined variety of *edentulus* (= *rugosus*), "connected by intergrades," and that they were the same species. He retained the two names, "thus avoiding inconvenience." Since only one species of *Strophitus* occurs in the Interior Basin and Atlantic Slope region, it is clear that, by priority, *undulatus* must be used.

Range. Interior Basin: Mississippi and Ohio drainages, from Central Texas to

Lake Winnipeg, Canada. Atlantic Slope: tributary of the upper Savannah River system, South Carolina, north to the St. Lawrence River system, Canada.

Specimens Examined

Savannah River System

Savannah River Drainage. *South Carolina:* Turkey Creek, 8 mi. NW Edgefield, Edgefield Co.

Cooper-Santee River System

Congaree River Drainage. *South Carolina:* Congaree River.

Cape Fear River System

Cape Fear River Drainage. *North Carolina:* Rocky River, 11 mi. N Sanford, Chatham Co.

Neuse River System

Neuse River Drainage. *North Carolina*: Beaverdam Creek, 4.75 mi. S Creedmoor (57); Crabtree Creek, 6 mi. NW Raleigh (38); Neuse River, Pooles Bridge; Swift Creek, 3 mi. SSW Garner (20); *all* Wake Co.

Pamlico River System

Tar River Drainage. *North Carolina*: Tar River, 2 mi. W Springhope, Nash Co.

Roanoke River System

Roanoke River Drainage. *Virginia*: Mason Creek, Salem; Roanoke River, Salem; *both* (Ortmann, 1919: 204); *both* Roanoke Co.

Chowan River System

Nottoway River Drainage. *Virginia*: Nottoway River, 3 mi. E Rawlings, Brunswick Co.

James River System

James River Drainage. *Virginia*: Calfpasture River, Goshen (Ortmann, 1919: 204); North [= Maury] River, 2 mi. WNW Lexington; North River, Buena Vista (Ortmann, 1919: 204); *all* Rockbridge Co. James River, opposite Maidens, Goochland Co. James River, Cartersville, Cumberland Co.

York River System

South Anna River Drainage. *Virginia*: [North Fork, S Anna River] Orange, Orange Co.

Rappahannock River System

Rapidan River Drainage. *Virginia*: Rapidan River, Rapidan, Culpeper Co. (Ortmann, 1919: 204).

Rappahannock River Drainage. *Virginia:* Rappahannock River, Remington, Fauquier Co. Mountain Run, Culpeper, Culpeper Co. *both* (Ortmann, 1919: 204).

Potomac River System

Potomac River Drainage. *West Virginia:* South Branch Potomac River, Romney, Hampshire Co. (Ortmann, 1919: 204). *Pennsylvania:* Conochocheague Creek, Greencastle and Scotland; East Branch, Little Antietam Creek, Waynesboro; *both* (Ortmann, 1919: 202); *both* Franklin Co. *Virginia:* North Fork, Shenandoah River, E Woodstock, Shenandoah Co. South River, Waynesboro, Augusta Co. (Ortmann, 1919: 204). South Fork, Shenandoah River, Elkton, Rockingham Co. (Ortmann, 1919: 204). *Maryland:* Potomac River, Hancock, Washington Co. (Ortmann, 1919: 204). Potomac River, Paton Id., .75 mi. W Point of Rocks, Frederick Co. *District of Columbia:* Aqueduct Lake.

Subfamily **Lampsilinae** (Ihering 1901) Ortmann 1910

Genus *Carunculina* Baker

Toxolasma Rafinesque 1831, Continuation of Monog. Bivalve Shells River Ohio (Phila.), p. 2. Species listed: *Unio cyclips; U. cinerescens; U. lividus; U. flexus; all* Rafinesque.

Type species, *Unio lividus* Rafinesque. By elimination, Frierson, 1914, Nautilus, 28: 7. Ortmann and Walker, 1922, Occ. Papers, Mus. Zool. Univ. Mich. no. 112, pp. 54, 55, show that *U. lividus* is a *nomen dubium* and that therefore *Toxolasma* must be disregarded.

Cornuculina [*sic*] Simpson 1898, *in* F. C. Baker,[1] Bull. Chicago Acad. Sci., 3(1): 109.
Type species, *Unio parvus* Barnes. Monotypic.
Carunculina, corrected in the index and on errata sheet, and reconfirmed by Simpson, 1900, Proc. United States Natl. Mus., 22: 563.
Ortmann, 1912, Ann. Carnegie Mus., 8: 377, *partim*. (Under *Eurynia*.)

Call (1896) monographed *Carunculina*, and indicated that it included only a few very variable species, and that most of its radiation was in the Interior Basin. He probably correctly reduced to synonymy many of the taxa subsequently recognized by Simpson (1914, 1: 148–161) and Frierson (1927: 87–89).

Carunculina pulla (Conrad)
Plate 17: 4–7

Unio pullus Conrad 1838, Monography Unionidae, no. 11, p. 100, pl. 55, fig. 2 (Wateree River, South Carolina; figured type ANSP [lost]; Warm Springs, [= Hot Springs, Madison Co.], North Carolina [Tennessee River system]; probably either *Villosa vaneuxemensis* (Lea) or *Carunculina glans* (Lea) (Ortmann and Walker, 1922: 55). Conrad (1838: 101) states that this specimen was seen subsequent to the preparation of the plate. Therefore, the type locality is here restricted to the former locality.)
Lampsilis pulla (Conrad). Simpson, 1914, Cat. Naiades, 1: 160.
Carunculina patrickae Bates 1966, Occ. Papers, Mus. Zool. Univ. Michigan, no. 646, pp. 1–9, 3 text figs., 1 pl. (Savannah River at approximately mile point 134.5 U.S. Army Corps of Engineers Map [= Johnsons Landing, 10 mi. W Allendale, Allendale Co.], on the South Carolina bank; holotype MZUM 85274).
Carunculina pulla (Conrad). Johnson, 1967, Nautilus, 80: 127, pl. 10, figs. 1–4.

Description. Shell small, seldom reaching over 35 mm in length. Outline of female long obovate, of male, elliptical. Valves subinflated, generally thin, somewhat thickened anteriorly. Anterior end regularly rounded; posterior end of females more broadly rounded and subtruncated below the medial line, somewhat pointed in males. Ventral margin straight in males. In females marsupial swelling causes the margin to be somewhat convex a little posterior of the center. Dorsal margin slightly curved, forming a distinct angle with the obliquely descending posterior margin. Posterior ridge double, sometimes broadly rounded, but more often both ridges very angular. Posterior slope slightly concave. Umbos prominent, not much elevated above the hinge line, located in the anterior third of the shell, their sculpture consisting of several concentric sharp ridges parallel to the growth lines, which curve upward to the posterior ridge. Periostracum generally with distinct growth lines, often satiny, generally blackish, though sometimes brownish, greenish, olivish, and with obscure very fine green rays.

Left valve with two raised triangular pseudocardinal teeth, one in front of the other, occasionally crenulate. Hinge line short and very narrow before two short, straight, lateral teeth. Right valve with one rather chunky, triangular pseudocardinal; one lateral tooth. Beak cavities shallow, with a few dorsal muscle scars under the hinge plate. Anterior adductor muscle scars well impressed, posterior ones faint. Pallial line distinct anteriorly. Nacre bluish white, pink to purplish, iridescent.

Length mm	Height mm	Width mm	
32.0	19.0	15.5	Savannah River, 10 mi. W Allendale, Allendale Co., South Carolina. Female.
22.0	13.5	10.0	As above. Male.
33.0	19.0	13.5	Wateree River, South Carolina. Male. [after Conrad].
25.0	17.0	11.0	University Lake, 1 mi. W Chapel Hill, Orange Co., North Carolina.

Habitat. Lives in shallow still water near the edges of streams and ponds, generally in mud, sometimes in sand.

Remarks. In the Atlantic Slope region

[1] H. B. Baker (1964, Nautilus, 78: 33) has pointed out that since Simpson contributed nothing in the original publication of this genus (under article 51 (c), 1964 edition of the International Code Zool. Nomen.), the authority for *Carunculina* must be F. C. Baker.

Carunculina pulla (Conrad) cannot be confused with any other species. The species of *Villosa* exhibit similar sexual dimorphism, but otherwise they are quite different from *pulla*. *Villosa delumbis* (Conrad) and *vibex* (Conrad) attain much larger size, have thinner, generally yellowish, distinctly rayed shells, whereas *pulla* is heavier for its size, blackish, and if rayed, only obscurely so. *Villosa villosa* (Lea), on the other hand, is broadly rayed, though the rays are sometimes visible only in transmitted light. *Villosa constricta* (Conrad) attains much larger size, has a similarly heavy shell, but it is shiny, has no distinct posterior ridge, and the females have a distinct "constriction" in the postbasal region.

Carunculina pulla most closely resembles *Carunculina parva* (Barnes) (= *C. paula* (Lea) Clench and Turner, 1956: 193) which is found throughout the Interior Basin and Apalachicolan region. The umbonal sculpture is similar, but *pulla* differs from *parva* by having heavy growth lines and a generally rougher periostracum; but more especially it differs by having a sharp posterior ridge, with a second, less prominent ridge above it. The posterior ridge is usually not present in typical *parva*, and when it is, it is generally not as acute as in *pulla*. Occasional specimens of *C. pulla* have an indistinct posterior ridge, as does one of the specimens figured. Nevertheless, the sharp posterior ridge is so generally present that *pulla*, with its relatively isolated distribution from *parva*, appears to be quite distinct from it. I have pointed out elsewhere (Johnson, 1967c) why it was not necessary to create a new taxon for this species.

Carunculina parva (Lea) is abundant in Black Creek, northern Florida, but no *Carunculina* have been reported from either the St. Marys or Satilla river systems, which are between Black Creek and the Altamaha River system. To the north, no *Carunculina* have been found on the Atlantic Slope beyond the Neuse River system.

It is likely that the ancestors of *C. pulla* entered the Southern Atlantic Slope region through a commingling of the headwaters of the Apalachicola and Savannah river systems.

Range. Southern Atlantic Slope: Altamaha River system, Georgia, north to the Neuse River system, North Carolina.

Specimens Examined

Altamaha River System

Ocmulgee River Drainage. *Georgia*: Ocmulgee River, below Lumber City, Telfair Co. (H. D. Athearn).

Altamaha River Drainage. *Georgia*: [Altamaha River] Darien, McIntosh Co. (USNM).

Savannah River System

Savannah River Drainage. *South Carolina:* Savannah River, approximately mile point 134.5 (U.S. Army Corps of Engineers Map) = Johnsons Landing, 10 mi. W Allendale, Allendale Co.

Santee River System

Wateree River Drainage. *North Carolina:* [Headwaters of] Catawba River; Pfeiffers Pond; Stewarts Pond; Bissels Pond; Beaver Creek; *all* Charlotte, Mecklenburg Co. (*all* ANSP). *South Carolina*: Wateree River (Conrad).

Cape Fear River System

New Hope River Drainage. *North Carolina:* University Lake, an impoundment on Morgan Creek, 1 mi. W Chapel Hill, Orange Co.

Neuse River System

Neuse River Drainage. *North Carolina*: Neuse River, Raleigh, Wake Co. (Lea).

Genus *Villosa* Frierson

Micromya Agassiz 1852, Archiv für Naturgeschichte, 18 (1): 47. Species listed: *Unio lapillus* Say, *Margaritana fabula* Lea, *M. curreyana* Lea, *non Micromya* Rondani 1840 (Insecta).

Type species, *Unio lapillus* Say. Subsequent designation, Herrmannsen, 1852, Indicis Generum Malacozoorum, Supp. et Corr., p. 83.

Ortmann, 1912, Ann. Carnegie Mus., 8: 337. *partim.*

Villosa Frierson, 1927, Check List North American Naiades, pp. 11, 80.

Type species, *Unio villosus* Wright. Original designation.

At this writing, it is impossible to tell how many species there are in *Villosa*. Frierson (1927: 70–79) includes under *Lampsilis,* subgenus *Ligumia*, many taxa which have been included by other authors under *Micromya* (= *Villosa*). Except for the type species, the taxa listed by Frierson (1927: 80, 81) under *Villosa* are species of *Carunculina*. In spite of the state of the synonymy of this genus, it is clear that the majority of its species occur in the Interior Basin.

Villosa villosa (Wright)
Plate 17: 8, 9

Unio villosus B. H. Wright 1898, Nautilus, 12: 32 (Suwannee River [Luraville], Suwannee Co., Florida; syntype USNM 150503, figured by Simpson, 1900, Proc. Acad. Nat. Sci. Phila., p. 77, pl. 1, fig. 1, selected as lectotype by Johnson, 1967, Occ. Papers on Moll., 3: 9, pl. 8, fig. 1).

Lampsilis villosus (Wright). Simpson, 1914, Cat. Naiades, 1: 143.

Villosa villosa (Wright). Clench and Turner, 1956, Bull. Florida State Mus., 1: 213, pl. 4, fig. 2.

Description. Shell usually small in size, seldom exceeding 60 mm in length. Outline long, elliptical. Valves subinflated, generally thin and translucent. Anterior end regularly rounded; posterior end of females slightly more broadly rounded, that of males quite pointed. Ventral margin almost always broadly curved except in females where a slight marsupial swelling, somewhat posterior of the center, renders it straight or slightly convex. Dorsal margin straight, with a very slight, if noticeable, angle where it meets the obliquely descending posterior margin. Hinge ligament small. Posterior ridge broadly rounded, double in the male; obscured by a slight marsupial swelling in the female. Posterior slope slightly concave. Umbos moderately swollen, slightly elevated above the hinge line, located in the anterior quarter of the shell, their sculpture consisting of several fine, low, slightly double-looped ridges. Surface of the shell with irregular growth lines, occasionally smooth and shiny, but usually covered with either rough or distinctly satiny periostracum, especially on the posterior slope. Periostracum sometimes subshiny, greenish yellow, dark greenish, or more often brownish black, the entire surface of the shell with broad green rays interspersed with narrow ones, sometimes only visible in transmitted light.

Left valve with two delicate pseudocardinal teeth, one in front of the other, the anterior one somewhat triangular, the hinder one inclined to be vestigial. Hinge line short and narrow before two short, straight lateral teeth. Right valve with two triangular, narrow, parallel pseudocardinals separated by a narrow pit, the more anterior tooth quite vestigial, sometimes absent; one low lateral tooth. Beak cavities shallow, a few dorsal muscle scars under the hinge plate. Anterior adductor muscle scars well impressed, posterior ones faint, if visible. Pallial line distinct anteriorly. Nacre bluish white, occasionally yellowish white, iridescent, especially posteriorly.

Length mm	Height mm	Width mm	
57	28	18	Suwannee River, Luraville, Suwannee Co., Florida. Lectotype. Female.
56	29	20	St. Marys River, Nassau Co., Florida. Female.
51	27	20	Spring Creek, Decatur Co., Georgia. Male.

Habitat. "Limited to spring-fed streams and clear rivers," Clench and Turner (1956: 214); but their report did not include the rather acid and muddy St. Marys River.

Remarks. Villosa villosa (Wright) bears a resemblance to *Villosa vibex* (Conrad), which is more widely distributed and extends over the whole range of *V. villosa*, as they both show similar sexual dimorphism. In the female of *villosa* there is, in general, less tendency for the postbasal swelling to extend below the ventral margin, and if inclined to be somewhat posteriorly pointed, the point is higher. The male is pointed posteriorly as in *vibex*, but the shell is proportionately longer. *V. villosa* often has a distinctive roughened periostracum which produces a satiny luster.

Range. Apalachicolan region: Apalachicola River system, east to the St. Marys River system, Georgia. Peninsular Florida.

Specimens Examined

St. Marys River System

St. Marys River Drainage. *Georgia*: St. Marys River, Traders Hill, Charleton Co. (MZUM). *Florida:* St. Marys River, Nassau Co. (USNM).

Villosa vibex (Conrad)
Plate 17: 10, 11
Plate 18: 1–3

Unio vibex Conrad, [May] 1834, New Fresh Water Shells United States, p. 31, pl. 4, fig. 3 (Black Warrior River, South of Blount's Spring [Blount Co.], Alabama; figured holotype ANSP 56488a). Published in May, *teste* Conrad, 1853, Proc. Acad. Nat. Sci. Phila., 6: 243.

Unio modioliformis Lea, [August or September] 1834, Trans. Amer. Philos. Soc., 5: 97, pl. 13, fig. 40 (Santee Canal, South Carolina; probable figured holotype USNM 85029 [differs slightly from figure]). Lea, 1834, Obs. Unio., 1: 209. Published in August or September, *teste* Lea, 1854, Proc. Acad. Nat. Sci. Phila., 7: 244.

Unio exiguus Lea 1840, Proc. Amer. Philos. Soc., 1: 287 (Chattahoochee River, near Columbus [Muscogee Co.], Georgia). Lea, 1842, Trans. Amer. Philos. Soc., 8: 191, pl. 7, fig. 1; figured holotype USNM 84974. Lea, 1842, Obs. Unio, 3: 29.

Unio stagnalis Conrad 1849, Proc. Acad. Nat. Sci. Phila., 4: 152 (inhabits mill ponds, Ogeechee River, Georgia, J. H. Couper [loaned]). Conrad, 1850, Jour. Acad. Nat. Sci. Phila., ser. 2, 1: 275, pl. 37, fig. 2; figured holotype MCZ 178778, purchased from J. H. Couper.

Unio prevostianus Lea 1852, Trans. Amer. Philos. Soc., 10: 269, pl. 19, fig. 24 (Eutowah [Etowah] River [North West], Georgia; figured holotype, C. M. Wheatley collection in ANSP [lost]). Lea, 1852, Obs. Unio, 5: 25.

Unio nigrinus Lea 1852, Trans. Amer. Philos. Soc., 10: 284, pl. 24, fig. 44 (West Florida; figured holotype USNM 86132). Lea, 1852, Obs. Unio, 5: 40.

Unio gracilior Lea 1856, Proc. Acad. Nat. Sci. Phila., 8: 262 (Buckhead Creek [Burke Co.]; Tobesaufke [Tobesofkee] Creek near Macon [Bibb Co.]; *both* Georgia). Lea, 1858, Jour. Acad. Nat. Sci. Phila., ser. 2, 4: 56, pl. 8, fig. 38; figured holotype USNM 85088 [localities not separated]. Lea, 1858, Obs. Unio, 6: 56.

Unio rutilans Lea 1856, Proc. Acad. Nat. Sci. Phila., 8: 262 Othcalooga [Oothkalooga] Creek, Gordon Co.; Columbus [Muscogee Co.]; *both* Georgia). Lea, 1858, Jour. Acad. Nat. Sci. Phila., ser. 2, 4: 59, pl. 9, fig. 41; figured holotype USNM 85093 from [Oothkalooga] Creek. Lea, 1858, Obs. Unio, 6: 59.

Unio subellipsis Lea 1856, Proc. Acad. Nat. Sci. Phila., 8: 262 (creeks near Columbus [Muscogee Co.], Georgia). Lea, 1858, Jour. Acad. Nat. Sci. Phila., ser. 2, 4: 62, pl. 10, fig. 44; figured holotype USNM 85095. Lea, 1858, Obs. Unio, 6: 62.

Unio sudus Lea 1857, Proc. Acad. Nat. Sci. Phila., 9: 170 (Dry Creek, near Columbus [Muscogee Co.]; Macon [Bibb Co.]; *both* Georgia). Lea, 1859, Jour. Acad. Nat. Sci. Phila., ser. 2, 4: 194, pl. 21, fig. 77; figured holotype USNM 85155 from Dry Creek. Lea, 1859, Obs. Unio, 7: 12.

Unio obfuscus Lea 1857, Proc. Acad. Nat. Sci. Phila., 9: 172 (Flint River, near Macon [Co.], Georgia). Lea, 1859, Jour. Acad. Nat. Sci. Phila., ser. 2, 4: 197, pl. 22, fig. 80; figured holotype USNM 85089. Lea, 1859, Obs. Unio, 7: 15.

Unio dispar Lea 1860, Proc. Acad. Nat. Sci. Phila., 12: 305 (Columbus [Muscogee Co.], Georgia). Lea, 1860, Jour. Acad. Nat. Sci. Phila., ser. 2, 4: 327, pl. 51, fig. 153; figured holotype USNM 85101. Lea, 1860, Obs. Unio, 8: 9.

Unio averillii Wright 1888, Proc. Acad. Nat. Sci. Phila., 40: 115, pl. 3, fig. 4 (Lake Ashby, Volusia Co., Florida; syntype figured by Simpson, 1892, Proc. United States Natl. Mus., 15: 414, pl. 56, fig. 6 [not located]). Lectotype USNM 91142,

selected by Johnson, 1967, Occ. Papers on Moll., 3: 5, pl. 7, fig. 4.

Villosa vibex (Conrad). Clench and Turner, 1956, Bull. Florida State Mus., 1: 209, pl. 4, fig. 4.

Description. Shell usually small in size, not exceeding 60 mm in length, though occasionally reaching 100 mm. Outline subelliptical. Valves subinflated, generally thin and translucent. Anterior end regularly rounded; posterior end of females more broadly rounded, somewhat pointed in males. Ventral margin straight or slightly curved in males, often slightly arcuate in females. Dorsal margin straight with a very slight, if noticeable, angle where it meets the obliquely descending posterior margin. Hinge ligament small. Posterior ridge broadly rounded. Posterior slope slightly concave, occasionally with faint wrinkles and ridges. Umbos moderately swollen, slightly elevated above the hinge line, located in the anterior quarter of the shell, their sculpture consisting of several fine, low, slightly double-looped ridges. Surface of the shell generally rather smooth, but roughened by periostracum posteriorly. Periostracum usually subshiny, greenish yellow, yellowish brown to almost black, the entire surface with numerous broad greenish rays, which in darker specimens can be seen in transmitted light.

Left valve with two delicate pseudocardinal teeth, one in front of the other, the anterior one somewhat triangular, the hinder one inclined to be vestigial. Hinge line rather long and very narrow before two short, straight lateral teeth. Right valve with two triangular, narrow, parallel pseudocardinals separated by a narrow pit, the more anterior tooth vestigial, sometimes absent; one lateral tooth. Beak cavities shallow, a few dorsal muscle scars under the hinge plate. Anterior adductor muscle scars well impressed, posterior ones faint, if visible. Pallial line distinct anteriorly. Nacre bluish white, sometimes pinkish or purple, iridescent posteriorly.

Length mm	Height mm	Width mm	
100	48	32	Ochee Creek, about 5 mi. SE Toomsboro, Wilkinson Co., Georgia. Male.
52	29	17	Mill Race, 2 mi. N Sardis, Burke Co., Georgia. Female.
48	27	17	As above. Male.

Habitat. Lives in mud or soft sand, particularly where rich in vegetable detritus, in small rivers and creeks.

Remarks. In the Southern Atlantic Slope region, *Villosa vibex* (Conrad) can be confused with *Villosa delumbis* (Conrad) with which it is often found living. *V. vibex* has broader, less distinct, green rays which are less inclined to be broken by sharp growth rests than those of *delumbis*. Sexual dimorphism is not as strongly developed in *vibex*. The males of both species tend to be somewhat pointed posteriorly. Females of *vibex* tend to be broadly rounded, rendering the shell slightly arcuate, while the females of *delumbis* are greatly inflated, with the posterior margin subangulate dorsally and truncate below. In the Apalachicolan region, *vibex* can be confused with *Villosa lienosa* (Conrad) which is allopatric with *V. delumbis*. See *Remarks* under *Villosa delumbis* (Conrad) on p. 376.

Range. West Gulf Coastal region, Alabama-Coosa River system, and Apalachicolan region: Pearl River system, Mississippi, east to the Suwanee River system, Florida. Peninsular Florida. Southern Atlantic Slope: Altamaha River system, Georgia, north to the coastal ponds of the Cape Fear River system, North Carolina.

Specimens Examined

Altamaha River System

Ocmulgee River Drainage. *Georgia*: Tobesofkee Creek, near Macon, Bibb Co. (USNM). Flat Creek, 2 mi. S Perry, Houston Co. Buck Creek, 5 mi. NW Hawkinsville; Limestone Creek, 4.3 mi. E Hawkinsville; Tucsawatchee Creek, 5 mi. SW Hawkinsville; Cedar Creek, Fountains

Mill, 7 mi. SW Hawkinsville; Mosquito Creek, 8 mi. SE Hawkinsville; *all* Pulaski Co. Brushy Creek, 8 mi. NW Abbeville, Wilcox Co. House Creek, Bowens Mill, 9 mi. N Fitzgerald; Dicksons Creek, 10 mi. NE Fitzgerald; *both* Ben Hill Co.

Little Ocmulgee River Drainage. *Georgia:* Little Ocmulgee River, 7 mi. NE Cochran, Bleckley Co. Alligator Creek, 2 mi. W Alamo, Wheeler Co. Gum Swamp Creek, 1 mi. N McRae, Telfair Co.

Oconee River Drainage. *Georgia*: Ochee Creek, about 5 mi. SE Toomsboro; Turkey Creek, 4 mi. NE Allentown; *both* Wilkinson Co. Ford Branch, 4 mi. W Dublin; Rocky Creek, 8 mi. W Dudley; *both* Laurens Co.

Ohoopee River Drainage. *Georgia*: Little Ohoopee River, 12 mi. NE Wrightsville; Little Ohoopee River, 2 mi. N Kite; Ohoopee River, 4 mi. S Wrightsville; *all* Johnson Co. Ohoopee River, Norristown, Emanuel Co.

Ogeechee River System

Ogeechee River Drainage. *Georgia*: Rocky Comfort Creek, 1 mi. N Louisville; Williamson Swamp Creek, Bartow; Nails Creek, 2 mi. S Bartow; Rocky Creek, 2 mi. S Wadley; *all* Jefferson Co. Barkcamp Creek, 7 mi. E Midville; Mill Creek, 5 mi. E Midville; Buckhead Creek, 4 mi. E Vidette; Rocky Creek, 5 mi. SW Waynesboro; *all* Burke Co. Chew Mill Creek, 8 mi. W Millen, Jenkins Co.

Savannah River System

Savannah River Drainage. *Georgia*: Brier Creek, 7.5 mi. NE Wrens, Jefferson Co. Mill Race, 2 mi. N Sardis; Beaverdam Creek, 7 mi. NW Girard; *both* Burke Co.

Combahee River System

Salkehatchee River Drainage. *South Carolina:* Little Salkehatchee River, 4 mi. N Ehrhardt, Bamberg Co. Salkehatchee River, Broxton Bridge; Whippy Swamp Creek, 2.5 mi. NE Crocketville; *both* Hampton Co.

Edisto River System

Edisto River Drainage. *South Carolina:* Edisto River.

Cooper-Santee River System

Wateree River Drainage. *South Carolina:* Wateree River, 2.5 mi. W Camden, Kershaw Co.

Santee River Drainage. *South Carolina:* Lake Moultrie, Cross, Berkeley Co. (USNM). Santee Canal (Lea).

Pedee River System

Lynches River Drainage. *South Carolina:* Lynches River, 2 mi. NE Bishopville, Lee Co.

Waccamaw River System

Waccamaw River Drainage. *North Carolina:* Lake Waccamaw, [town of] Lake Waccamaw, Columbus Co.

Cape Fear River System

Cape Fear River Drainage. *North Carolina:* Sprunts Pond [not located] (USNM); stream below Greenfield Mill Pond, Wilmington (ANSP); *both* New Hanover Co.

Villosa delumbis (Conrad)
Plate 18: 4–8

Unio delumbis Conrad 1834, New Fresh Water Shells United States, p. 35, pl. 5, fig. 3 (small streams near Cooper River, South Carolina; figured type not in ANSP [lost]).

Unio tenerus Ravenel 1834, Cat. Recent Shells Cabinet Edmund Ravenel, p. 7 (Cooper River, South Carolina) [*nomen nudum*]. Simpson 1892, Proc. United States Natl. Mus., 15: 416, pl. 58, figs. 5, 8 (South Carolina; figured syntype USNM 85030 [male]; [Savannah River], Georgia; figured syntype USNM 85032 [female]). Walker, 1919, Occ. Papers, Mus. Zool. Univ. Mich. no. 74, p. 1, pl. 1, figs. 1–6.

Unio vaughanianus Lea 1838, Trans. Amer. Philos. Soc., 6: 5, pl. 3, fig. 5 (Sawney's Creek, near [about 8 mi. NW] Camden [Kershaw Co.], South Carolina; two syntypes USNM 86106, one a bit smaller than the figure, the other with the outline of the figure, but with less prominent rays. The figure appears to be a composite.) Lea, 1838, Obs. Unio, 2: 5.

Unio ogeecheensis Conrad 1849, Proc. Acad. Nat.

Sci. Phila., 4: 153 (Ogeechee River, Georgia, J. H. Couper [loaned]). Conrad, 1850, Jour. Acad. Nat. Sci. Phila., ser. 2, 1: 275, pl. 37, figs. 3–4; figured syntype, fig. 3, MCZ 146971 purchased from J. H. Couper, selected as lectotype by Johnson, 1956, Bull. Mus. Comp. Zool., 115: 126.

Unio concavus Lea 1852, Trans. Amer. Philos. Soc., 10: 260, pl. 15, fig. 11 (Abbeville District [Savannah River drainage], South Carolina; figured holotype USNM 85154). Lea, 1852, Obs. Unio, 5: 16.

Unio proximus Lea 1852, Proc. Amer. Philos. Soc., 5: 252 (Georgia). Lea, 1852, Trans. Amer. Philos. Soc., 10: 271, pl. 20, fig. 27; figured holotype USNM 85131. Lea, 1852, Obs. Unio, 5: 27.

Unio contiguus Lea 1861, Proc. Acad. Nat. Sci. Phila., 13: 392 (Stewarts Mill Dam, Union Co., North Carolina). Lea, 1862, Jour. Acad. Nat. Sci. Phila., ser. 2, 5: 199, pl. 28, fig. 268; figured holotype USNM 85120. Lea, 1863, Obs. Unio, 9: 21.

Unio genuinus Lea 1868, Proc. Acad. Nat. Sci. Phila., 20: 161 (Bissels Pond, Charlotte [Mecklenburg Co.] North Carolina). Lea, 1868, Jour. Acad. Nat. Sci. Phila., ser. 2, 6: 305, pl. 46; fig. 117, figured holotype USNM 85123. Lea, 1869, Obs. Unio, 12: 64.

Description. Shell usually small in size, seldom exceeding 60 mm in length. Outline of female long obovate; of male long elliptical. Valves subinflated, generally thin and translucent. Anterior end regularly rounded; posterior end of females more broadly rounded and subtruncated below the medial line, somewhat pointed in males. Ventral margin straight in males, in females marsupial swelling causes the margin to be somewhat convex a little posterior of the center. Dorsal margin straight forming a sharp angle with the obliquely descending posterior margin. Posterior ridge broadly rounded. Posterior slope slightly concave, occasionally with faint ridges and wrinkles. Umbos moderately swollen, slightly elevated above the hinge line, located in the anterior third of the shell, their sculpture consisting of several fine, low, slightly double-looped ridges. Surface of the shell generally rather smooth and shiny, but roughened by periostracum posteriorly especially on the posterior slope. Periostracum often subshiny, greenish yellow, brownish, or greenish, the entire surface with narrow, sometimes very narrow, greenish rays which are broken by growth rests to form concentric bands.

Left valve with two delicate pseudocardinal teeth, one in front of the other, the anterior one somewhat triangular, the hinder one inclined to be vestigial. Hinge line rather long and very narrow before two short, straight lateral teeth. Right valve with two triangular, narrow, parallel pseudocardinals separated by a narrow pit; the more anterior tooth vestigial, sometimes absent; one lateral tooth. Beak cavities shallow, a few dorsal muscle scars under the hinge plate. Anterior adductor muscle scars well impressed, posterior ones faint, if visible. Pallial line distinct anteriorly. Nacre sometimes dirty white or pinkish, but usually bluish white and iridescent.

Length mm	Height mm	Width mm	
64	39	30	Ogeechee River, Georgia. Lectotype of *U. ogeecheensis* Conrad. Female.
57	35	19	Mill Race, 2 mi. N Sardis, Burke Co., Georgia. Female.
53	30	19	As above. Male.

Habitat. Lives in mud or soft sand, particularly where rich in vegetable detritus, in small rivers and creeks.

Remarks. In the Southern Atlantic Slope region, *Villosa delumbis* (Conrad) can be confused only with *Villosa vibex* (Conrad) under which see: *Remarks* on p. 374.

Villosa delumbis (Conrad) is very close to *Villosa lienosa* (Conrad) of the Apalachicolan region. Both species are similarly shaped and the females show the same sexual dimorphism. *V. lienosa* has a much heavier shell; the posterior ridge, while rounded, tends to be faintly biangulate. The periostracum is usually black or very dark yellowish green, and when visible the rays are solid green. The nacre is often pinkish or coppery. *V. delumbis* has a thinner shell, there is scarcely ever a hint

of the posterior ridge being faintly biangulate, the periostracum is usually a light yellow or light greenish yellow, and the rays are almost always distinct and characteristically broken by growth rests. The nacre is very seldom pinkish.

Although the figured type of *V. delumbis* has been lost, the life size figure, with its distinct, narrow rays, clearly distinguishes it from *vibex*, and it corresponds almost exactly in outline with the male shell figured in this report.

Range. Southern Atlantic Slope: Altamaha River system, Georgia, north to the Neuse River system, North Carolina.

Specimens Examined

Altamaha River System

Ocmulgee River Drainage. *Georgia*: Macon, Bibb Co. Echeconnee Creek, Echeconnee, Houston Co. Buck Creek, 5 mi. NW Hawkinsville; Limestone Creek, 4.3 mi. E Hawkinsville; Tucsawhatchee Creek, 5 mi. SW Hawkinsville; Cedar Creek, 8 mi. SW Hawkinsville; *all* Pulaski Co.

Oconee River Drainage. *Georgia*: Ochee Creek, about 5 mi. SE Toomsboro; Turkey Creek, 4 mi. NE Allentown; *both* Wilkinson Co. Ford Branch, 4 mi. W Dublin; Palmetto Creek, 7 mi. S Dublin; *both* Laurens Co.

Ohoopee River Drainage. *Georgia*: Ohoopee River, 4 mi. S Wrightsville; Little Ohoopee River, 1 mi. E Kite; *both* Johnson Co. Ohoopee River, 1 mi. E Adrian; Ohoopee River, Norristown; Yam Grande Creek, 3 mi. W Swainsboro; *all* Emanuel Co.

Altamaha River Drainage. *Georgia*: Darien, McIntosh Co. (USNM).

Ogeechee River System

Ogeechee River Drainage. *Georgia*: Ogeechee River, Shoals, Warren Co. Ogeechee River, 4 mi. SW Mitchell, Glascock Co. Williamson Swamp Creek, Bartow, Jefferson Co. Barkcamp Creek, 7 mi. E Midville; Mill Creek, 5 mi. E Midville; *both* Burke Co. Chew Mill Creek, 8 mi. W Millen, Jenkins Co. Ogeechee River, Scarboro; Ogeechee River, bridge 1 mi. S Dover; Ogeechee River, 1.5 mi. SW Oliver; *all* Screven Co. (*all* MZUM). Ogeechee River, bridge 1.5 mi. E Blitchton; Ogeechee River, Jinks Bridge [Rte. 16]; Ogeechee River, Morgan Bridge, 14 mi. SE Pembroke; Ogeechee River, mouth of Arnold Lake; Jones Lake; *all* Bryan Co. (*all* MZUM).

Savannah River System

Broad River Drainage. *Georgia*: Broad River, Elbert, Huguenot Co. (USNM) Broad River, Lincoln Co.

Savannah River Drainage. *Georgia*: Savannah River, Augusta, Richmond Co. *South Carolina:* Savannah River, 2 mi. SW Millettville (MZUM); Savannah River, Johnsons Landing, 10 mi. W Allendale; *both* Allendale Co. *Georgia:* Savannah River, 7.5 mi. NE Shell Bluff; Brier Creek, 6 mi. N Waynesboro; outlet of Waynesboro Lake, Waynesboro; Mill Race, 2 mi. N Sardis; *all* Burke Co.

Combahee River System

Salkehatchee River Drainage. *South Carolina:* Pauline Cave, near Kline, Barnwell Co. (MZUM).

Edisto River System

Edisto River Drainage. *South Carolina:* Snake Swamp Creek, Orangeburg Co. 6 mi. NE Bamberg, Bamberg Co. Edisto River, Canadys Landing, 8 mi. SW St. George, Dorchester Co. Edisto River, 1 mi. E Jacksonboro, Colleton Co. (MZUM).

Cooper-Santee River System

Congaree River Drainage. *South Carolina:* Congaree River.

Catawba River Drainage. *North Carolina:* Long Creek; Catawba River; Bissels Pond, Charlotte; Pfeiffers Pond, Charlotte (ANSP); Flannigans Pond, Charlotte (ANSP); *all* Mecklenburg Co. [Ten Mile

Creek] of Catawba River, Wolfsville [7 mi. W Monroe], Union Co. (MZUM).

Wateree River Drainage. *South Carolina:* Sawneys Creek, about 8 mi. NW Camden, Kershaw Co. (USNM).

Cooper River Drainage. *South Carolina:* near Cooper River (Conrad).

Pedee River System

Yadkin River Drainage. *North Carolina:* Stewarts Mill Dam, Union Co. (USNM).

Waccamaw River System

Waccamaw River Drainage. *North Carolina:* drainage canal beside Lake Waccamaw, 1 mi. NNW Dupree Landing, Columbus Co.

Cape Fear River System

Cape Fear River Drainage. *North Carolina*: University Lake, an impoundment on Morgan Creek, 1 mi. W Chapel Hill, Orange Co. Rocky River, 11 mi. N Sanford, Chatham Co. (MZUM). North East Cape Fear River, Dublin Co. (MZUM). Greenfield Mill Pond, Wilmington, New Hanover Co. (USNM).

Neuse River System

Neuse River Drainage. *North Carolina*: North Flat River, 5.5 mi. S Roxboro Center, Person Co. (81). Neuse River (USNM).

Villosa constricta (Conrad)
Plate 18: 9–10

Unio lienosus constrictus Conrad 1838, Monography Unionidae North America, no. 10, p. 91, pl. 49, fig. 4 (North [= Maury] River, Rockbridge Co., Virginia; figured holotype ANSP 20423, now ANSP 56465a.)

Unio genthii Lea 1857, Proc. Acad. Nat. Sci. Phila., 9: 85 (Catawba River, Gaston Co.; Deep River, Gulf [Chatham Co.]; *both* North Carolina). Lea, 1862, Jour. Acad. Nat. Sci. Phila., ser. 2, 5: 57, pl. 2, fig. 204; figured holotype USNM 84834, labeled, Roanoke River, Raleigh, North Carolina, Prof. Emmons. (This locality is nonexistent. There is no way to tell which locality the type was from; so it is assumed here that since it was probably Prof. Emmons' specimen that was figured, it was from Deep River, Gulf, Chatham Co., North Carolina, and the type locality is, here, so restricted.) Lea, 1862, Obs. Unio, 8: 61.

Lampsilis constricta (Conrad). Simpson, 1914, Cat. Naiades, 1: 111.

Eurynia (*Micromya*) *constricta* (Conrad). Ortmann, 1915, Nautilus, 29: 66.

Description. Shell small in size, seldom exceeding 50 mm in length. Outline of female short obovate; of male subelliptical. Valves not much inflated, rather heavy and strong. Anterior end regularly rounded; posterior end of females more broadly rounded and pointed a little more than midway up from the base, truncated below the medial line. In mature specimens there is a rather distinct "constriction" in the middle of this truncation which marks the boundary between the branchial opening and the papillar part of the mantle edge in front of it; somewhat pointed in males, the point being generally less than midway up from the base. Ventral margin quite convex in females, slightly convex in males. Dorsal margin rather rounded, forming a more or less distinct angle with the obliquely descending posterior margin. Posterior ridge broadly rounded. Posterior slope slightly concave, occasionally with fine radiating wrinkles. Umbos not much swollen, slightly elevated above the hinge line, located in the anterior quarter of the shell, their sculpture consisting of evenly double-looped ridges. Surface of the shell generally rather smooth and shiny, sometimes roughened with concentric growth lines. Periostracum often subshiny, yellowish green, or bottle green, becoming brownish with age, generally with distinct, but very fine, green rays over the entire surface.

Left valve with two rather heavy pseudocardinal teeth, one in front of the other, both rather triangular. Hinge line very short and very narrow before two straight lateral teeth. Right valve with two pseudocardinals, the posterior one chunky and serrated, the more anterior tooth vestigial; one lateral tooth. Beak cavities shallow,

a few dorsal muscle scars under the hinge plate. Anterior adductor muscle scars well impressed, posterior ones faint, if visible. Pallial line generally distinct anteriorly. Nacre sometimes dirty white or yellowish, especially toward the beak cavities, but usually bluish white and iridescent.

Length mm	Height mm	Width mm	
49.0	28.0	17.0	Pedlar River, 1 mi. W Pleasantview, Amherst Co., Virginia. Male.
41.4	27.0	16.0	North River, Rockbridge Co., Virginia. Female. Holotype of *Unio constrictus* Conrad.
39.0	27.0	18.0	[Deep River, Gulf, Chatham Co.], North Carolina. Male. Holotype of *Unio genthii* Lea.

Breeding season. The breeding season begins in August and ends in June. Glochidia subspatulate, higher than long. Length 0.21 mm, height 0.27 mm (Ortmann, 1915: 66, 67).

Habitat. Lives in sand in rather swift, flowing rivers.

Remarks. Villosa constricta (Conrad) of the Southern Atlantic Slope region does not much resemble any other unionid found there. There is often quite a bit of difference in the degree of inflation and form of the shell, but it differs from all of the other Atlantic Slope *Villosa* in the shape of the postbasal swelling which generally does not project beyond the base line of the shell, and in the emargination behind the swelling. For its size *constricta* is much heavier and stronger than any other *Villosa* in the region under study, and has a distinctive yellowish green or shiny dark chestnut-brown periostracum, and the female has a distinct constriction in the postbasal region. Females of *Carunculina pulla* (Conrad) show a similar sexual dimorphism, but they lack the constriction. In addition, *pulla* usually has a sharp double posterior ridge, a rough periostracum and if rayed at all, obscurely so, whereas *constricta* has a broadly rounded posterior ridge and a generally smooth, shiny surface that is distinctly rayed.

Villosa constricta (Conrad) is allopatric with *Villosa vanuxemensis* (Lea) (Simpson, 1914, 1: 105) of the Cumberland and Tennessee rivers. The constriction found rather regularly in old females of *constricta* is not as well developed in *vanuxemensis*, and the latter has a distinct nacre color (usually an unreliable character) which varies from dirty purplish white through salmon-tinted to dark purple, usually darker toward the beak cavity of the shell, whereas the nacre color of *constricta* is dirty white, bluish white or yellowish toward the beak cavities. Ortmann (1915: 66) collected a number of specimens of *vanuxemensis* on September 17, 1912 in the North Fork, Holston River, Saltville, Smyth Co., Virginia, and at once recognized its affinity with *constricta*.

Range. Southern Atlantic Slope: Catawba River, North Carolina, of the upper Cooper-Santee River system, north to the James River system, Virginia.

Specimens Examined

Cooper-Santee River System

Catawba River Drainage. *North Carolina:* Catawba River, Gaston Co. (Lea). Beaver Creek [Gaston Co.] (MZUM). Long Creek [Mecklenburg Co.] (MZUM). [Ten Mile Creek] of Catawba River, Wolfsville [7 mi. W Monroe], Union Co. (USNM).

Cape Fear River System

Deep River Drainage. *North Carolina*: Deep River, Gulf, Chatham Co. (Lea).

Cape Fear River Drainage. *North Carolina:* Rocky River, 11 mi. N Sanford, Chatham Co. (MZUM).

Neuse River System

Neuse River Drainage. *North Carolina*: North Flat River, 5.5 mi. S Roxboro, Person Co. (81). Eno River, 1.8 mi. S Cedar Grove (122); Eno River, Hillsboro; *both*

Orange Co. Eno River, 6 mi. NW Durham (113); Fork, Little River, 11 mi. NNW Durham (101); *both* Durham Co. Neuse River, 6 mi. E Raleigh; Hare-Snipe Creek, 6.25 mi. NW Raleigh (37); Little River, Tarpleys Mill, 2 mi. NE Wendell (5); *all* Wake Co.

Pamlico River System

Tar River Drainage. *North Carolina*: Tar River, 2 mi. ENE Bunn, Franklin Co. Chicod Creek, Pitt Co. (MZUM).

Roanoke River System

Staunton River Drainage. *Virginia*: Mason Creek, near Roanoke River, Salem; Tinker Creek, Roanoke (MZUM); *both* Roanoke Co.

James River System

James River Drainage. *Virginia*: Dunlap Creek (MZUM); Jackson River, Covington (MZUM); Cowpasture River, near Longdale (MZUM); *all* Alleghany Co. Calfpasture River, Goshen (MZUM); North [= Maury] River, 2 mi. WNW Lexington; *both* Rockbridge Co. James River, Buchanan, Botetourt Co. Pedlar River, 1 mi. W Pleasantview, Amherst Co. James River, opposite Beaver Creek, 6 mi. E Lynchburg, Campbell Co. (MZUM). James River, Cartersville, Cumberland Co. James River, opposite Maidens, Goochland Co. James River, Richmond, Henrico Co. (ANSP).

Genus *Ligumia* Swainson

Ligumia Swainson 1840, Treatise on Malacology, pp. 268, 274, 378.

Type species, [*Unio*] *recta* Lamarck. Original designation, p. 274.

Ortmann, 1912, Ann. Carnegie Mus., 8: 338, *partim*.

Ortmann and Walker, 1922, Occ. Papers, Mus. Zool. Univ. Mich., no. 112, p. 59.

Frierson (1927: 70–79) includes many taxa in this genus. Most of them have been placed by subsequent authors under *Lampsilis s. s.* and *Villosa*. It appears that *Ligumia* contains two species, *L. recta* (Lamarck) (Ortmann, 1919: 276, pl. 16, figs. 12, 13) (the so-called subspecies *latissima* (Rafinesque) is an ecophenotype, occurring in rivers) and *L. nasuta* (Say).

Ligumia nasuta (Say)
Plate 19: 1, 2

Unio nasutus Say 1817, Nicholson's Encyclopedia, 2 [no pagination], pl. 4, fig. 1 (Delaware and Schuylkill [rivers near Philadelphia, Philadelphia Co., Pennsylvania]; type, ANSP [lost]).

Obliquaria attentuata Rafinesque 1820, Ann. Gén. des Sci. Physiques (Bruxelles), 5: 304 (la fleuve Hudson [New York]; type, not in ANSP [lost]).

Unio rostrata Valenciennes 1827, *in* Humboldt and Bonpland, Voyage aux Régions Equinoxiales du Nouveau Continent, pt. 2, 2: 233, pl. 53, fig. 3 (Philadelphia vicinis [near] [Philadelphia Co., Pennsylvania]; type [location unknown]).

Unio vaughanianus Sowerby 1868, Conch. Iconica, 16, *Unio*, pl. 61, fig. 308, *non* Lea, 1838.

Unio fisherianus Kuester 1860, Conch. Cabinet, 9, pt. 2, pl. 68, fig. 6, *non* Lea, 1838.

Lampsilis nasuta (Say). Simpson, 1914, Cat. Naiades, 1: 97.

Eurynia nasuta (Say). Ortmann, 1919, Mem. Carnegie Mus., 8: 271, pl. 16, figs. 10, 11.

Ligumia nasuta (Say). Clarke and Berg, 1959, Cornell Univ. Exp. Sta. Mem. 367, p. 51, fig. 54.

Description. Shell generally medium in size throughout most of its range, usually not exceeding 80 mm in length, though reaching over 110 mm in a few localities. Outline elongated, subelliptical, or sublanceolate; distinctly over twice as long as high. Valves usually subcompressed, thin to subsolid, inequilateral. Anterior end regularly rounded; posterior end elongated and bluntly pointed. Ventral margin curved. Dorsal margin straight, slightly curved, forming a distinct angle, at least in immatures, with the obliquely descending posterior slope. Hinge ligament rather long and low. Posterior ridge distinct and angular, becoming toward the umbos broader, more rounded, and indistinct. Posterior slope slightly concave, near the umbos becoming flatter or even somewhat

convex posteriorly. Umbos very low, located in the anterior quarter of the shell, their sculpture consisting of fine close ridges which are looped in front and run parallel to the axis of the shell behind. Surface of the shell with irregular growth lines, sometimes with a few nearly vertical ridges below the posterior ridge. Periostracum usually fine, subshiny, greenish yellow, dark olive to brownish, often with distinct fine rays, especially posteriorly.

Left valve with two compressed pseudocardinal teeth, one in front of the other, both subtriangular and crenulated; no interdentum; two long straight laterals. Right valve with two pseudocardinals, the posterior one triangular, the more anterior one low and vestigial; one lateral tooth. Beak cavities very shallow, with a few dorsal muscle scars. Anterior adductor muscle scars well impressed; posterior ones often scarcely visible. Pallial line distinct anteriorly. Nacre bluish white, often cream color or salmon, especially toward the beak cavity, posteriorly iridescent.

Sexual differences well marked in the shell. The male shell tapers uniformly behind into a point, but the female is distinctly produced in the postbasal region, behind which the ventral margin slopes up more acutely than in the male, and is straight or concave.

Length mm	Height mm	Width mm	
112	44	28	Connecticut River, Hartford, Hartford Co., Connecticut. Male.
66	29	14	Potomac River, Washington, District of Columbia. Female.
62	25	12	As above. Male.

Anatomy. Discussed by Ortmann (1911: 343); discussed and figured by Reardon (1929: 7, pl. 2, figs. 1–10). The glochidia are subovate, with an undulate hinge line, and measure 0.25 mm in length and 0.29 mm in height. The host fish is unknown.

Breeding season. Ortmann (1919: 272) indicates from specimens he examined in Lake Erie that this species breeds from August until the following June.

Habitat. Lives in sand and mud, mostly in protected areas in ponds, lakes, canals, and in slack water areas of streams.

Remarks. Ligumia nasuta (Say) of the upper Ohio River drainage and Atlantic Slope region is distinguishable from any other North American unionid by its usually distinctly lance-head shaped posterior end. On the Atlantic Slope the male shell can be confused with *Elliptio lanceolata* (Lea), but the latter does not have the same distinct pattern of rays, nor the dull olive green color. Also the nacre of *nasuta* is generally silvery white or cream colored, whereas that of *lanceolata* may be coppery or purple. The females of *nasuta* have a distinct expansion in the postbasal region which render them more easily distinguishable from *lanceolata* than the male shell.

Clarke and Berg (1959: 51), apparently following Simpson (1914, 1: 97), give the southern range of this species as North Carolina. Simpson's record appears to be based on series of rather posteriorly produced specimens of *Elliptio lanceolata* (Lea) from Wilmington, New Hanover Co., North Carolina. *Ligumia nasuta* is decidedly part of the northern element of the Atlantic Slope fauna, the James River, Virginia, being its southernmost record. (Conrad, 1836: 38, pl. 18, fig. 1, figures a female specimen from the James River, but it has not been collected there since his time.) As observed by Conrad, *nasuta* does not go very far up into the rivers in the southern part of its range, and we are led by Conrad to believe that his record from the James is from the tidewater region. It is abundant in the Potomac River in the tidewater region, but is not found very far up the river. Ortmann (1919: 275) found the distribution to be similar in Pennsylvania.

Range. Atlantic Slope: James River system, Virginia, north to the St. Lawrence

River system, Canada, westward through the Mohawk River and Erie [now New York State Barge] Canal, *both* New York. Interior Basin: Lake Erie, Ohio, and Michigan.

Specimens Examined

James River System

James River Drainage. *Virgina*: James River (Conrad).

Potomac River System

Potomac River Drainage. *District of Columbia:* Potomac River.

Genus *Lampsilis* Rafinesque

Lampsilis Rafinesque 1820, Ann. Gén. des Sci. Physiques (Bruxelles), 5: 298. Species listed: *Lampsilis cardium* Rafinesque, *Lampsilis ovata* (Say), *Lampsilis fasciola* Rafinesque.

Type species, *Unio ovatus* Say. Subsequent designation, Herrmannsen, 1847, Indicis Generum Malacozoorum, 1: 575. Ortmann, 1912, Ann. Carnegie Mus., 8: 345.

Aeglia Swainson 1840, Treatise on Malacology, pp. 265, 378. Species listed: *Ae. ovata* (Say), *occidens* (Lea).

Type species, *Unio ovatus* Say. Subsequent designation, Herrmannsen, 1846, Indicis Generum Malacozoorum, 1: 20.

Subgenus *Lampsilis s.s.*

All of the species described in this paper belong to *Lampsilis s. s.* Frierson (1927: 67–86) lists ten other subgenera, three of which are of his own creation. One of them, *Villosa*, is now used as a replacement name for *Micromya* Agassiz (see under *Villosa* on p. 371. *Ligumia* Swainson now replaces *Eurynia* Rafinesque. To comment on the other subgenera is not in the scope of this paper, but on cursory examination, the present author disagrees substantially with Frierson's classification, both on a generic and specific level.

Lampsilis s. s., while clearly of Interior Basin origin, appears to have speciated about equally there and in the combined Apalachicolan and Atlantic Slope regions.

Lampsilis (Lampsilis) cariosa (Say)
Plate 19: 3–5

Unio cariosus Say 1817, Nicholson's Encyclopedia, 2 [no pagination], pl. 3, fig. 2 (Delaware and Schuylkill Rivers; [Susquehanna River], Wilkes Barre; [Luzerne Co.; *all* Pennsylvania]; type, ANSP [lost]). The type locality was restricted to: Schuylkill River, near Philadelphia, Pennsylvania, and a neotype MCZ 178839 was selected by Johnson (1947, Occ. Papers on Moll., 1: 148, pl. 19, fig. 1).

Lampsilis pallida Rafinesque 1820, Ann. Gén. des Sci. Physiques (Bruxelles), 5: 299 (Hudson River, [New York]; type not in ANSP [lost]).

Unio ovata Valenciennes 1827, *in* Humboldt and Bonpland, Voyage aux Régions Equinoxiales du Nouveau Continent, pt. 2, 2: 226, pl. 50, figs. 1 a–c, (près de Washington [District of Columbia]; type [location unknown]) *non* Say 1817.

Unio crocatus Lea 1841, Proc. Amer. Philos. Soc., 2: 31 (Savannah River, Georgia). Lea, 1842, Trans. Amer. Philos. Soc., 8: 238, pl. 22, fig. 52; figured holotype USNM 84908. The lectotype selected by Johnson (1947, Occ. Papers on Moll., 1: 156) but not figured, is invalid. The holotype which was catalogued under the same number has since been located. Lea, 1842, Obs. Unio, 3: 76.

Unio oratus Conrad 1849, Proc. Acad. Nat. Sci. Phila., 4: 153 (Flint River, Georgia; here restricted to: Ogeechee River, Georgia[1]). Conrad 1850, Jour. Acad. Nat. Sci. Phila., ser. 2, 1: 267, pl. 37, fig. 6; type, coll. of J. H. Couper [lost].

Lampsilis cariosa (Say). Simpson, 1914, Cat. Naiades, 1: 43. Ortmann, 1919, Mem. Carnegie Mus., 8: 313, pl. 20, figs. 3–5. Johnson, 1947, Occ. Papers Moll., 1: 145, pl. 19, figs. 1–2. Clarke and Berg, 1959, Cornell Univ. Exp. Sta. Mem., no. 367, p. 54, figs. 59–60. Clarke and Rick, 1963, Natl. Mus. Canada, Bull. no. 189, p. 27, pl. 1, fig. 3.

Description. Shell usually medium, though reaching 130 mm in length. Outline of male elliptical and somewhat elongate; of female subovate, or obovate, rather short and high. Valves inequilateral, some-

[1] Also described on the same page in both publications is *Unio contrarius* = *Lampsilis claibornensis* (Lea) with Ogeechee River, Georgia, as the type locality. The localities for the two species are obviously transposed, since *oratus* is not found in the Flint River, but in the Ogeechee River, and *contrarius* is found in the Flint River and not in the Ogeechee River.

what inflated; moderately heavy. Anterior end regularly rounded; posterior end more broadly rounded and somewhat pointed in the male, truncated in the female. Ventral margin slightly curved. Dorsal margin straight, terminating in a broad angle with the obliquely descending posterior margin. Hinge ligament prominent, running under the umbos and appearing anteriorly. Posterior ridge rounded and poorly defined. Posterior slope slightly convex, usually with a few faint ridges and wrinkles. Umbos moderately swollen, slightly raised above the hinge line, located somewhat anterior to the middle of the shell, their sculpture consisting of four or five wavy recurved ridges. Surface of the shell generally smooth except for a few growth ridges. Periostracum usually shiny, bright wax or straw yellow, infrequently greenish yellow, becoming a dirty brownish yellow or reddish brown in matures. Green or blackish rays, when present, usually restricted to the posterior slope.

Left valve with two compressed, serrated pseudocardinal teeth, one in front of the other, the anterior one somewhat triangular, the hinder one lower, but chunky, located directly under the umbo. Hinge line rounded, with a considerable interdentum under the umbo before two short lateral teeth. Right valve with two opposing pseudocardinals, the anterior one low and laminate, the other higher, chunky and serrated; one lateral tooth, sharply truncated behind. Beak cavities moderately deep, with deep dorsal muscle scars. Anterior adductor muscle scars well impressed, posterior ones less so. Pallial line distinct. Nacre bluish white or tinged with salmon.

Length mm	Height mm	Width mm	
130	85	56	Savannah River, 7 mi. NE Newington, Screven Co., Georgia. Male.
98	62	42	As above. Male.
98	69	45	As above. Female.

Anatomy. Figured by Lea (1838, pl. 15, fig. 45). Ortmann (1912: 353) says that the anatomy of *L. cariosa* is similar to that of *Lampsilis ovata ventricosa* (Barnes).

Breeding season. According to Ortmann (1919: 315) this species is probably brady-tictic.

Habitat. The largest examples are found in the swift waters of large rivers on sand bars or gravelly bottoms, though it also occurs in smaller creeks and, occasionally, in ponds.

Remarks. In the Atlantic Slope region, *Lampsilis cariosa* (Say) can be confused with *L. dolabraeformis* (Lea) of the Altamaha River system, but the latter species has much higher umbos and a very sharp posterior ridge, especially toward the umbos, whereas in *cariosa* the umbos are slightly elevated above the hinge line, and the posterior ridge is poorly defined.

Lampsilis cariosa has been most often confused with *L. ochracea* (Say) with which it is sometimes found throughout its range. In general, *L. ochracea* has a thinner, smaller shell, and unlike *cariosa*, which is rarely rayed except posteriorly, *ochracea* is often rayed over the entire surface of the shell and it has a rougher, duller, more greenish periostracum. The hinges are quite different. The pseudocardinals of *L. cariosa* are pyramidal, and an interdentum is present; but in *L. ochracea* the pseudocardinals are lamellate, almost parallel to the hinge line, and there is no interdentum.

Lampsilis cariosa is found with *Lampsilis ovata* (Say) in the Potomac River system, where the latter was introduced, and in the St. Lawrence River system. While the two species are close, they are distinct. *L. ovata* has a rather sharp posterior ridge, is somewhat inflated, has a dull olivaceous tint to the shell, and is inclined to be rayed over the entire surface. *L. cariosa* has a poorly defined posterior ridge, is not especially inflated, usually has a distinctive bright yellow, glossy periostracum, and rays when present are usually confined to the posterior slope.

Range. Atlantic Slope: Ogeechee River system, Georgia, north to the Sydney River, Nova Scotia (Clarke and Rick, 1963: 27), and in the St. Lawrence River system, Canada, westward to the Madawaska River, Ontario, of the lower Ottawa River drainage.

Specimens Examined

Ogeechee River System

Ogeechee River Drainage. *Georgia*: Ogeechee River, Shoals, Warren Co. Ogeechee River, Scarboro, Screven Co. (MZUM). Ogeechee River, mouth of Arnold Lake [Bryan Co.] (MZUM).

Savannah River System

Savannah River Drainage. *South Carolina:* Abbeville District (USNM). Edgefield District. Savannah River, 2 mi. SW Millettville (ANSP); Savannah River, Johnsons Landing, 10 mi. W Allendale; Savannah River, Kingjaw Point, 10 mi. WSW Allendale (ANSP); *all* Allendale Co. *Georgia:* Savannah River, 7.5 mi. NE Shell Bluff; Savannah River, 6 mi. NE Girard; *both* Burke Co. Below Haga Slage Landing, E Sylvania (ANSP); Savannah River, 7 mi. NE Newington; *both* Screven Co. Savannah River, in sandbank, Savannah, Chatham Co. (MZUM).

Cooper-Santee River System

Congaree River Drainage. *South Carolina:* Congaree River.

Wateree River Drainage. *South Carolina:* Wateree River, 2.5 mi. W Camden, Kershaw Co.

Santee River Drainage. *South Carolina:* Santee River, Wilsons Landing, 5 mi. NW Pineville (ANSP); below Santee River Dam, near St. Stephens; *both* Berkeley Co.

Waccamaw River System

Waccamaw River Drainage. *South Carolina:* Waccamaw River, Wachasaw Landing, 2 mi. W Murrells Inlet, Georgetown Co.

Cape Fear River System

Cape Fear River Drainage. *North Carolina:* Cape Fear River, Cumberland Co. (USNM).

Neuse River System

Neuse River Drainage. *North Carolina*: Eno River, 6 mi. NNW Durham, Durham Co. (112). Neuse River [6 mi. E] Raleigh; tributary of Swift Creek, 5 mi. SW Raleigh (22); *both* Wake Co.

Pamlico River System

Tar River Drainage. *North Carolina*: Tar River, 2 mi. W Springhope, Nash Co.

Chowan River System

Nottoway River Drainage. *Virginia*: Nottoway River, 3 mi. E Rawlings, Brunswick Co.

York River System

Pamunkey River Drainage. *Virginia*: Pamunkey River, 2 mi. N Hanover, Hanover Co.

Potomac River System

Potomac River Drainage. *Maryland*: Monocacy River, 2 mi. W Mt. Pleasant, Frederick Co. Potomac River, Cabin John, Montgomery Co. (Ortmann, 1919: 316). Potomac River, Great Falls, Fairfax Co. *District of Columbia:* Potomac River.

Lampsilis (Lampsilis) dolabraeformis (Lea) Plate 20: 1–4

Unio dolabraeformis Lea 1838, Trans. Amer. Philos. Soc., 6: 103, pl. 24, fig. 113 (Altamaha River, Liberty [now Long] Co.; Altamaha River, near Darien [McIntosh Co]; *both* Georgia; figured holotype USNM 84888). Lea, 1838, Obs. Unio, 2: 103.

Lampsilis dolabraeformis (Lea). Simpson, 1914, Cat. Naiades, 1: 46.

Description. Shell large, often exceeding 130 mm in length. Outline of male

elliptical and somewhat elongate; of female obovate, rather short and high. Valves inflated, rather heavy. Anterior end regularly rounded; posterior end more broadly rounded and somewhat pointed in the male, truncated in the female. Ventral margin slightly curved. Dorsal margin straight, terminating in a broad angle with the obliquely descending posterior margin. Hinge ligament prominent, running under the umbos and appearing anteriorly. Posterior ridge very sharp and angular near the umbos, gradually becoming less so toward the ventral margin, especially in older individuals. Posterior slope slightly convex, usually with a few faint ridges and wrinkles. Umbos swollen, much elevated above the hinge line, located somewhat anterior to the middle of the shell, their sculpture consisting of four or five rather evenly raised bars which terminate at the posterior ridge. Surface of the shell smooth except for a few concentric ridges anteriorly. Periostracum usually shiny, yellowish green, sometimes becoming chestnut brown or black in matures. The posterior slope usually has a concentration of green or black rays which extend with less frequency over the posterior portion of the disk.

Left valve with two compressed pseudocardinal teeth, one in front of the other, the anterior one higher. Sometimes these are broken into three imperfect teeth or are united in one narrow ridge. Hinge line rounded, with a considerable interdentum under the umbo before two short lateral teeth. Right valve with two opposing pseudocardinals, the anterior one low and laminate, the other higher, chunky, and serrated; one lateral tooth, sharply truncated behind. Beak cavities deep and wide, with deep dorsal muscle scars under the pseudocardinal teeth. Anterior adductor muscle scars deep, posterior ones distinct, but not impressed. Pallial line distinct. Nacre white, bluish white, or pinkish, usually iridescent.

Length mm	Height mm	Width mm	
129	91	64	Altamaha River, 4 mi. N Jesup, Wayne Co., Georgia. Male.
108	78	55	As above. Female.
91	69	49	Altamaha River, 10 mi. N Baxley, Appling Co., Georgia. Female.
79	63	50	As above. Male.

Anatomy. Discussed by Lea (1863: 413).

Habitat. Usually found in sand bars, where the river is wide and the water is rather swift, though occasionally found in mud.

Remarks. Lampsilis dolabraeformis (Lea) is known only from the Altamaha River system. It is close to *Lampsilis cariosa* (Say) which is found throughout the Atlantic Slope region, but differs from *cariosa* by having umbos which are much higher and a posterior ridge which is considerably sharper, especially toward the umbos.

In the Apalachicolan region, *L. dolabraeformis* resembles *L. excavatus* (Lea). The latter does not extend east of the Escambia River system. It is a smaller species than *dolabraeformis*, the umbos are not as high, the posterior ridge is not quite as sharp, especially in females, and the entire surface has wide green or blackish rays which are often broken into concentric bands of green. In *dolabraeformis* the rays are restricted to the area toward the posterior ridge and posterior slope, and the rays are fine, sharp, and not broken. *L. dolabraeformis* also resembles *L. binominatus* Simpson (Johnson, 1967b: 9) of the Upper Apalachicola River system. The rays are very similar, but in *binominatus* they cover the entire surface. Further, *binominatus* is a much smaller species, which does not have the high umbos or sharp posterior ridge of *dolabraeformis*.

Simpson (1914, 1: 46) reports *dolabraeformis* from the Ogeechee and Savannah River systems, but the specimens in the United States National Museum are all *Lampsilis cariosa* (Say).

Range. Southern Atlantic Slope: restricted to the Altamaha River system, Georgia.

Specimens Examined

Altamaha River System

Ocmulgee River Drainage. *Georgia*: Ocmulgee River, Hawkinsville, Pulaski Co. Ocmulgee River, 1.5 mi. S Jacksonville; Gum Swamp Creek, 1 mi. N McRae; Ocmulgee River, 1 mi. S Lumber City; *all* Telfair Co.

Oconee River Drainage. *Georgia*: Oconee River, 2.5 mi. N Glenwood; Ochwalkee Creek, 2 mi. E Glenwood; Oconee River, 8 mi. SW Soperton; *all* Wheeler Co.

Altamaha River Drainage. *Georgia*: Altamaha River, 7 mi. N Hazlehurst, Jeff Davis Co. Altamaha River, 10 mi. N Baxley; Altamaha River, 10 mi. NE Surrency; *both* Appling Co. Altamaha River, "Riverside Park," 4 mi. N Jesup, Wayne Co. Altamaha River, 3 mi. NW Everett City, Glynn Co. Altamaha River, Fort Barrington; Altamaha River, Hopeton, near Darien; *both* McIntosh Co.

Lampsilis (Lampsilis) ovata (Say)
Plate 21: 1–2

Unio ovatus Say 1817, Nicholson's Encyclopedia, 2 [no pagination], pl. 2, Fig. 7 (Ohio River and its tributary streams; type, ANSP [lost]). Neotype Senckenberg Mus. 4338 [not seen] selected, but not figured, by Haas, 1930, Senckenbergiana, 12: 328.

Lampsilis cardium Rafinesque 1820, Ann. Gén. des Sci. Physiques (Bruxelles), 5: 298, pl. 30, figs. 16–19; ([Ohio River]: supposed type ANSP 20210 *teste* Vanatta, 1915, Proc. Acad. Nat. Sci. Phila., 66: 5511).

Unio ventricosus Barnes 1823, Amer. Jour. Sci., 6: 267, pl. 13, fig. 14 (The Wisconsan [Wisconsin River] near Prairie du Chien [Crawford Co., Wisconsin] type, Lyceum of Natural History of New York [destroyed by fire]).

Unio occidens Lea 1829, Trans. Amer. Philos. Soc., 3: 435, pl. 10, fig. 16 (Ohio; figured holotype USNM 84866). Lea, 1834, Obs. Unio, 1: 49.

Unio subovatus Lea 1831, Trans. Amer. Philos. Soc., 4: 118, pl. 18, fig. 46 (Ohio River; figured holotype USNM 84509). Lea, 1834, Obs. Unio, 1: 128.

Unio lenis Conrad 1838, Monography Unionidae, no. 11, back cover. Conrad, 1840, *op. cit.*, no. 12, p. 106, pl. 58, fig. 2 (upper part of White River, Illinois, possible type ANSP 42307, [smaller than figured specimen]).

Unio canadensis Lea 1857, Proc. Acad. Nat. Sci. Phila., 9: 85 (St. Lawrence River, near Montreal [Quebec], Canada). Lea, 1860, Jour. Acad. Nat. Sci. Phila., ser. 2, 4: 268, pl. 44, fig. 148; figured holotype USNM 84503. Lea, 1860, Obs. Unio, 7: 86.

Unio latissimus Sowerby 1868, Conch. Iconica, 16, *Unio*, pl. 66 fig. 337 (United States, Sowerby coll. not in BMNH [lost]).

Lampsilis ventricosa lurida Simpson 1914, Cat. Naiades, 1: 41 (throughout the St. Lawrence drainage; holotype USNM [not located]).

Lampsilis ventricosa cohongoronta Ortmann 1912, Nautilus, 26: 53 (no type selected. Lectotype, selected by Parodiz (1967: 28) Carnegie Mus. 61.3999, from Potomac River, Hancock, Washington Co., Maryland), pl. 21: 1; allotype 61.4000, pl. 21:2.

Lampsilis ventricosa winnebagoensis Baker 1928, Bull. Wisconsin Geol. Nat. Hist. Survey, no. 70(2), p. 291, pl. 94, figs. 1–4 (Winnebago Lake, near Oshkosh [Winnebago Co.], Wisconsin; holotype MZUM 209219).

Lampsilis ventricosa perglobosa Baker 1928, Bull. Wisconsin Geol. Nat. Hist. Survey, no. 70(2), p. 285, pl. 93, figs. 1–4 (Lake Pepin, near Lake City [Wabasha Co.], Wisconsin; holotype MZUM 209195).

Lampsilis ovata (Say). Ortmann, 1919, Mem. Carnegie Mus., 8: 297, pl. 17, figs. 8, 9; pl. 18, figs. 1–3.

Lampsilis ovata ventricosa (Barnes). Ortmann, 1919, Mem. Carnegie Mus., 8: 301, pl. 18, fig. 4 pl. 19, figs. 1–3. Clarke and Berg, 1959, Cornell Univ. Exp. Sta. Mem., no. 367, p. 55, figs. 47, 48.

Description. Shell usually medium, though reaching 140 mm in length. Outline of male elliptical or subelliptical, of female subovate, rather short and high. Valves somewhat to considerably inflated, thin when young, becoming thick with age, inequilateral. Anterior end regularly rounded; posterior end more broadly rounded and somewhat pointed in the male, truncated in the female. Ventral margin slightly

curved. Dorsal margin short and straight, terminating in a broad angle or gentle curve with the obliquely descending posterior margin. Hinge ligament prominent, occupying most of the dorsal margin. Posterior ridge variable; it may be rounded and poorly defined, though often becoming distinct toward the umbos, and in some habitats the posterior ridge becomes very sharp toward the umbos. Posterior slope varies from gently convex to almost flat, or even concave toward the umbos. Umbos moderately swollen, slightly raised above the hinge line, located somewhat anterior to the middle of the shell, their sculpture consisting of four or five rather coarse bars, of which the second and third have a slight tendency to fall into two loops, with a small sinus in the middle, while the first, fourth, and fifth bars are indistinct. Surface of the shell generally smooth except for growth ridges. Periostracum usually light or dark yellowish green to olive brown. Dark green or blackish rays which are straight and continuous, finer or broader, often cover the entire surface or only part of it, but some rays are almost always present. On the posterior slope the periostracum is less smooth and usually darker.

Left valve with two slightly compressed pseudocardinal teeth, one in front of the other, the anterior one somewhat triangular, the hinder one lower, located directly under the umbos, both teeth quite chunky. Hinge line rounded with a narrow interdentum under the umbos; two short lateral teeth. Right valve with two opposing pseudocardinals, the anterior one low and laminate, the other higher, quite chunky, and serrated; one lateral tooth, sharply truncated behind. Beak cavities moderately deep, with deep dorsal muscle scars. Anterior adductor muscle scars well impressed, posterior ones less so. Pallial line distinct. Nacre silvery or bluish white, sometimes suffused with pink or purple.

Length mm	Height mm	Width mm	
115	78	56	Potomac River, Hancock, Washington Co., Maryland. Female.
111	73	47	South Branch, Potomac River, South Branch, Hampshire Co., West Virginia. Male. Carnegie Mus.
95	60	41	Potomac River, Hancock, Washington Co., Maryland. Lectotype of *L. v. cohongoronta* Ortmann. Male.
87	52	57	As above. Allotype. Female.

Anatomy. Discussed by Ortmann (1911: 351). The glochidia are subelliptical, with a straight line hinge, without hooks, and measure 0.25 mm in length and 0.29 mm in height. Coker, et al. (1921: 153) report the following fish as hosts: bluegill, *Lepomis macrochirus* Rafinesque; white crappie, *Pomoxis annularis* Rafinesque; largemouth bass, *Micropterus salmoides* (Lacépède); smallmouth bass, *M. dolomieui dolomieui* Lacépède; yellow perch, *Perca flavescens* (Mitchill); and yellow pikeperch, *Stizostedion vitreum* (Mitchill).

Breeding season. According to Ortmann (1919: 298, 303, 308) this species is bradytictic.

Habitat. Lives in rivers and creeks on gravel, sand, or even mud bottoms; also occurs in lakes.

Remarks. Lampsilis ovata (Say) is a species of the Interior Basin and St. Lawrence River system which was accidently introduced into the Shenandoah River in 1889 and in other parts of the Potomac River system in 1894, while in the larval stage, on species of bass and other fishes that were transplanted at those times from the west. On the Atlantic Slope *ovata* can be confused only with *Lampsilis cariosa* (Say), with which it is now found in the lower Potomac River system. *L. ovata* generally has a sharper posterior ridge, especially near the umbos, tends to be inflated, has a dull olivaceous tint to the shell, is inclined to be rayed over the entire surface, and has rather heavy chunky

pseudocardinals. *L. cariosa* always has a poorly defined posterior ridge, is not much inflated, usually has a distinctive bright waxy yellow glossy periostracum. Rays when present are usually confined to the posterior slope, and the pseudocardinals are less chunky than those of *ovata*.

The present synonymy of *ovata* may not be the last word spoken on the subject (the author is not yet prepared to comment on the validity of *Unio satur* Lea, which is found in the Western Gulf Coastal region), but it is an attempt to use modern systematic concepts. Ortmann (1919: 298, 303) clearly states that *L. ovata* occurs in large rivers and gradually gives way to *ovata ventricosa* in smaller rivers and streams, that numerous intergrades occur in intermediate areas and, further, that this is a general phenomenon and occurs in widely separated streams. Van der Schalie (1938: 70) discusses a similar change from *ovata ventricosa*, the river form, to the *ovata canadensis*, the lake form, which also intergrade. Goodrich and van der Schalie (1944: 315) again note that, "as one progresses into the headwaters the sharp posterior ridge of the true *ovata* is seen to round off and we pass gradually to the more common form of the species in Indiana, known as *Lampsilis ovata ventricosa* (Barnes)." Cvancara's (1963) work appears to indicate that *ovata* and *ventricosa* are ecophenotypes.

Ortmann (1912: 53) proposed *cohongoronta* as a variety of *Lampsilis ventricosa*, "on account of the small size, the shorter and higher outline, and somewhat more distinct posterior ridge." He found no difference in the anatomy or glochidia from *L. ventricosa*.

When Ortmann wrote in 1912, *Lampsilis ovata* was found on the Atlantic Slope only in the Great Allegheny Valley, an area from which *cariosa* has never been reported. Since that time *ovata* has spread throughout the Potomac River, having reached Great Falls, Maryland, by 1915 (Marshall, 1917: 40). Writing again, Marshall (1930: 19) indicated that *cariosa* was being replaced by *ovata*. This is confirmed by collections made in the Potomac River in 1965 by S. L. H. Fuller.

Range. Interior Basin: Mississippi and Ohio drainages. St. Lawrence drainage from Lake Superior to the Ottawa River and Lake Champlain. Hudson Bay drainage. Northern Atlantic Slope: restricted to the Potomac River system, Maryland (introduced).

Specimens Examined

Potomac River System

Potomac River Drainage. *West Virginia:* South Branch, Potomac River, Romney (Carnegie Mus.); South Branch, Potomac River, South Branch [Depot = French Station] (Carnegie Mus.); *both* Hampshire Co. Cacapon River, 1 mi. above confluence with Potomac River, Morgan Co. (USNM). *Maryland:* Potomac River, Hancock, Washington Co. (Carnegie Mus.). *Virginia:* Shenandoah River, Harpers Ferry, Jefferson Co. (Carnegie Mus.). *Maryland:* Potomac River, Paton Island, 0.75 mi. W Point of Rocks, Frederick Co. Potomac River, 2.5 mi. WSW Dickerson; Potomac River, Harrison Island, 5 mi. above Great Falls (USNM); Potomac River, Great Falls (USNM); Chesapeake and Ohio Canal, Great Falls (USNM); *all* Montgomery Co.

Lampsilis (Lampsilis) ochracea (Say)
Plate 21: 4, 5

Mytilus fluviatilis Gmelin 1791, Systema Naturae, ed. 13, 1, pl. 6, p. 3359 (Europae, aquis dulcibus [erroneous], type [probably based on Lister's figure only]) refers to: Lister, 1685, Synopsis Methodicae Conchyliorum, pl. 157, fig. 12 (Virginia; figured specimen Oxford Univ. Mus. [probably lost] *teste* Dance, 1966, Shell Collecting, p. 292). Conrad (1836, Monography Unionidae, no. 4, p. 37) considered Lister's figure to represent *Lampsilis ochracea* (Say), but the figure is sufficiently ambiguous to have subsequently allowed Isaac Lea to claim successfully, for over fifty years, that *M. fluviatilis* Gmelin was *Anodonta cataracta*

Say. Since Lister makes no reference to dentition or lack of it, his figure cannot be positively identified. Gmelin's name is certainly a *nomen dubium*.

Unio ochraceus Say 1817, Nicholson's Encyclopedia, 2 [no pagination], pl. 3 fig. 8 (Delaware and Schuylkill Rivers; type ANSP [lost]). The type locality was restricted to Schuylkill River, near Philadelphia, Pennsylvania, and a neotype MCZ 178838 was selected by Johnson, 1947, Occ. Papers on Moll., 1: 153, pl. 20, fig. 2.

Lampsilis rosea Rafinesque 1820, Ann. Gén. des Sci. Physiques (Bruxelles), 5: 229 (Hudson River [New York]; type not in ANSP [lost]).

Unio rosaceus Conrad 1849, Proc. Acad. Nat. Sci. Phila., 4: 153 (Savannah River, Georgia, J. H. Couper [loaned]). Conrad, 1850, Jour. Acad. Nat. Sci. Phila., ser. 2, 1: 275, pl. 37, fig. 5; figured holotype MCZ 178779, purchased from J. H. Couper.

Lampsilis ochracea (Say), Simpson, 1914, Cat. Naiades, 1: 49. Ortmann, 1919, Mem. Carnegie Mus., 8: 318, pl. 20, figs. 6, 7. Johnson, 1947, Occ. Papers on Moll., 1: 150, pl. 20, figs. 1–2. Clarke and Berg, 1959, Cornell Univ. Exp. Sta. Mem., no. 367, p. 57, figs. 55, 56. Athearn and Clarke, 1962, Natl. Mus. Canada, Bull. no. 183, p. 30, pl. 4, figs. 3, 4.

Description. Shell usually small, seldom exceeding 70 mm in length. Outline of male elliptical and somewhat elongate; of female subovate, rather short and high. Valves inequilateral, subinflated, rather thin, though strong, sometimes translucent. Anterior end regularly rounded; posterior end more broadly rounded and somewhat pointed in the male, truncated in the female. Ventral margin usually straight or slightly curved, sometimes concave in females. Dorsal margin straight or slightly curved, terminating in a broad angle with the obliquely descending posterior margin. Hinge ligament prominent, running under the umbos and appearing anteriorly. Posterior ridge rounded and generally poorly defined. Posterior slope slightly convex, usually with a few faint ridges and wrinkles. Umbos moderately swollen, slightly raised above the hinge line, located somewhat anterior to the middle of the shell, their sculpture consisting of four or five wavy recurved ridges. Surface of the shell generally smooth in the region of the disk, becoming roughened with periostracum posteriorly. Periostracum usually subshiny, brownish olive, brownish, greenish yellow, reddish yellow, or yellow. Dull, rather fine, greenish rays sometimes found over the entire surface of the shell, especially in immatures.

Left valve with two compressed, serrated pseudocardinal teeth, one in front of the other, the anterior one somewhat triangular, the hinder one lower, inclined to be vestigial. Hinge line rather long and narrow before two short, curved lateral teeth. Right valve with two triangular, narrow, parallel pseudocardinals separated by a deep narrow pit, the more anterior tooth inclined to be vestigial; one lateral tooth. Beak cavities shallow, with deep dorsal muscle scars. Anterior adductor muscle scars well impressed, posterior ones less so. Pallial line not very distinct. Nacre white, bluish white, or pinkish, usually iridescent.

Length mm	Height mm	Width mm	
73	44	27	Savannah River, Georgia. Holotype of *U. rosaceus* Conrad. Male.
50	31	19	Schuylkill River, near Philadelphia, Pennsylvania. Neotype. Male.
54	38	24	Halfway Pond, Plymouth, Plymouth Co., Massachusetts. Female.

Anatomy. Figured by Lea (1838: pl. 15, fig. 44) and described (1863: 455) also by Reardon (1929: 1, pl. 1, figs. 1–10). The host fish is unknown, but since *ochracea* is generally restricted to the lower regions of streams or bodies of water directly connected with the ocean, it may, like *Anodonta implicata* Say, parasitize a migratory fish.

Breeding season. Lea (1863: 455) found this species gravid in the autumn. I found gravid females on May 3, 1943 in Plymouth, Massachusetts. It is probably bradytictic.

Habitat. Lives in sand or mud in ponds, canals, and the lower portions of rivers to-

ward the tidal region in areas where the current is not strong.

Remarks. In the Atlantic Slope region, *Lampsilis ochracea* (Say) has been confused with *L. cariosa* (Say), but *ochracea* has a thinner, smaller shell and, unlike *cariosa* which is rarely rayed, *ochracea* is often rayed over the entire surface. It has a rougher, duller, more greenish periostracum. The hinges are quite different. The pseudocardinals of *cariosa* are pyramidal and an interdentum is present, but in *ochracea* the pseudocardinals are lamellate, almost parallel to the hinge line, and there is no interdentum.

Lampsilis ochracea may also be mistaken for immature *Lampsilis splendida* (Lea), but only in that the shells of both may be rayed over the entire surface. The rays of *ochracea* are finer, and the shell is more yellowish, whereas that of *splendida* is more brownish, less delicate, and more inflated.

Simpson (1914: 49) gives the range of this species as from "New England to the Ogeechee River, Georgia." The specimen in the United States National Museum on which he based the Ogeechee record from Le Conte appears to be a young *cariosa*. Unfortunately, in none of the major museums are there any precisely labeled specimens of *ochracea* from the Savannah River, the apparent southern limit of its distribution. Conrad (1836: 37) reports *ochracea* as occurring in, "most of the tide waters north of Savannah River."

Range. Atlantic Slope: Savannah River system, Georgia, north to River Herbert, Nova Scotia (Athearn and Clarke, 1962: 30).

Specimens Examined

Savannah River System

Savannah River Drainage. *Georgia*: Savannah River (MCZ and USNM).

Waccamaw River System

Waccamaw River Drainage. *North Carolina*: Lake Waccamaw, [town of] Lake Waccamaw; drainage canal, beside Lake Waccamaw, 1 mi. NNW Dupree Landing; *both* Columbus Co. *South Carolina:* Waccamaw River, Wachasaw Landing, 2 mi. W Murrells Inlet, Georgetown Co.

Pamlico River System

Tar River Drainage. *North Carolina*: Tar River, Old Sparta, 3.5 mi. W Pinetops, Edgecombe Co. Tar River, Bruce, 9 mi. NW Greenville, Pitt Co.

Roanoke River System

Roanoke River Drainage. *North Carolina*: Roanoke River, Weldon, Halifax Co. (USNM).

James River System

Appomattox River Drainage. *Virginia*: Petersburg, Dinwiddie Co. (USMN).

James River Drainage. *Virginia*: James River (MCZ and USNM).

York River System

Mattaponi River Drainage. *Virginia*: Mantapike Creek, Mantapike, King and Queen Co. (USNM).

York River Drainage. *Virginia*: York River (MZUM).

Potomac River System

Potomac River Drainage. *Virginia*: Potomac River, Great Falls, Fairfax Co. *District of Columbia*: Potomac River. Anacostia River. *Virginia:* Canal, Alexandria (MZUM); Little Hunting Creek, near Mt. Vernon (MZUM); *both* Fairfax Co.

Lampsilis (Lampsilis) radiata radiata (Gmelin) Plate 22: 1–3

Mya radiata Gmelin 1791, Systema Naturae, ed. 13, 1, pt. 6, p. 3220 (Malabariae [erroneous]) refers to: Martini and Chemnitz, 1782, Conch. Cabinet, 6, pl. 2, fig. 7 ([source of Gmelin's locality]; figured specimen Spengler colln. Copenhagen, [lost] *teste* Haas, 1913, Vidensk. Meddr. Dansk naturh. Foren. [Copenhagen], 65: 59); also Lister, 1685, Synopsis Methodicae Conchyliorum, pl. 152, fig. 7 (Virginia; figured specimen, Oxford Univ. Mus. [probably lost]

teste, Dance, 1966, Shell Collecting, p. 292). The figure in Martini and Chemnitz is here selected as the type figure, and the type locality, following Lister and Simpson (1914, Cat. Naiades, 1: 64), is here restricted to Potomac River, District of Columbia (approximately opposite, Fairfax Co., Virginia).

Unio luteola Lamarck 1819, Hist. Nat. des Animaux sans Vertèbres, 6: 79 (la rivière Susquehana [Susquehanna River, Pennsylvania] et celle Mohancks [Mohawk River, New York]; measured holotype Paris Museum, figured by Wheeler, 1963, Nautilus, 77: 58, pl. on p. 59, figs. 1–2. Refigured by Johnson, 1969, Nautilus, 83: 54, fig. 11, the type locality was restricted to the Susquehanna River, Columbia, York Co., Pennsylvania).

Unio lineata 'Valenciennes' Bory de St. Vincent 1827, Encyclopédie Méthodique, 2 of atlas, explanation of pls., p. 151, pl. 248, fig. 5 (no locality, type [presumed lost]). [Named from figure published in 1797.]

Unio tenebrosus Conrad 1834, New Fresh Water Shells United States, p. 42, pl. 7, fig. 1 (Rappahannock [*sic*] River, near Falmouth, Stafford Co., Virginia; type presumably in Poulson colln., ANSP [lost]).

Unio melinus Conrad 1838, Monography Unionidae, no. 11, p. 101, pl. 56, fig. 1 (Salina Lake [Onondaga Co.], New York; type, not in ANSP, presumed lost).

Unio boydianus Lea 1840, Proc. Amer. Philos. Soc., p. 286 (Oak Orchard Creek, Orleans Co., New York). Lea, 1843, Trans. Amer. Philos. Soc., 8: 216, pl. 16, fig. 32; figured holotype USNM 86126). Lea, 1942, Obs. Unio, 3: 54.

Unio rosaceus De Kay 1843, Zool. New York, Moll., pt. 5, p. 192, pl. 39, figs. 355, 356; pl. 40, fig. 357 (Seneca Lake [North Western], New York; lectotype, here selected, USNM 678303, formerly New York State Cabinet 391, specimen figured on pl. 39, fig. 356).

Mya oblongata Wood 1856, Index Testaceologicus, ed. Hanley, p. 199, Supplement, pl. 1, fig. 2 (North America, type [lost]).

Unio elongata S. G. Goodrich 1859, Illustrated Natural History, 2: 523, text fig. (No locality, type [probably not saved].)

Unio obliquiradiatus Reeve 1856, Conch. Iconica, 16, *Unio*, pl. 29, figs. 151 (Hab ?, Mus. Cuming, type [not in BMNH, lost]).

Unio conspicuus Lea 1872, Proc. Acad. Nat. Sci. Phila., 24: 156 (Yadkin River, Salisbury, [Rowan Co.], North Carolina). Lea, 1874, Jour. Acad. Nat. Sci. Phila., ser. 2, 8: 34, pl. 11, fig. 31; figured holotype USNM 85056. Lea, 1874, Obs. Unio, 13: 38.

Unio virginiana Simpson, 1900, Proc. United States Natl. Mus., 22: 536, *non* Lamarck 1819. Lamarck's type examined and identified as *Elliptio complanatus* Solander [*sic*] *teste* Johnson, 1953, Nautilus, 66: 95.

Lampsilis radiata (Gmelin). Simpson, 1914, Cat. Naiades, 1: 64. Ortmann, 1919, Mem. Carnegie Mus., 8: 292, pl. 17, figs. 6, 7.

Lampsilis radiata oneidensis Baker 1916, Nautilus, 30: 74, pl. 2 (Oneida Lake, Central New York; syntypes, New York State College of Forestry, Syracuse, New York; ANSP 114854; MZUM).

Unio virginea Frierson 1927, Check List North American Naiades, p. 72, error for *Unio virginiana* Lamarck 1819, *non* Lamarck.

Lampsilis radiata radiata (Gmelin). Clarke and Berg, 1959, Cornell Univ. Exp. Sta. Mem. no. 367, p. 58, fig. 53. Athearn and Clarke, 1962, Natl. Mus. Canada, Bull. no. 183, p. 31, pl. 4, figs. 5, 6.

Lampsilis radiata var. *conspicua* (Lea). Simpson, 1914, Cat. Naiades, 1: 66.

Description. Shell large, often reaching over 100 mm in length. Outline subelliptical or subovate, moderately elongated, distinctly over one and a half times as long as high. Valves generally subinflated, though occasionally quite inflated, and solid. Anterior end regularly rounded; posterior end more broadly rounded, and in females often somewhat expanded in the postbasal region, though not uniformly so. Ventral margin generally regularly curved, sometimes straight, roughly parallel to the almost straight dorsal margin which forms a blunt angle with the posterior margin in immatures, and becomes almost imperceptible with age. Hinge ligament prominent. Posterior ridge feeble or wanting. Posterior slope broad and undistinguished. Umbos rather sharp, but not full or high, their sculpture consisting of six to ten double-looped bars, with a distinct re-entering angle in the middle. The posterior loop is slightly angular and indistinct on the posterior slope. Surface roughened by close concentric wrinkles of periostracum, generally yellowish or brownish green, with dark greenish or blackish rays, both narrow and wide, over the entire surface.

Left valve with two stumpy pseudocardinal teeth, both rather triangular and crenulate. No interdentum. Two long, slightly curved lateral teeth. Right valve

with one rather high, triangular pseudocardinal, and a vestigial one before it; one lateral tooth. Beak cavities very shallow, with a few dorsal muscle scars. Anterior and posterior adductor muscle scars and pallial line all distinct. Nacre generally white, bluish white, sometimes tinted with pink or salmon, sometimes quite pink or salmon.

Length mm	Height mm	Width mm	
138	86	46	Lake Michie, 12 mi. NNE Durham, Durham Co., North Carolina. Male.
112	64	39	Yadkin River, near Salisbury, Rowan Co., North Carolina. Holotype of *U. conspicuus* Lea. Male.
99	52	29	Susquehanna River, Columbia, York Co., Pennsylvania. Male.
84	49	27	Potomac River, Washington, District of Columbia. Male.
62	39	20	As above. Female.

Anatomy. Figured by Lea (1838, pl. 15, figs. 48, 49). According to Ortmann (1911: 349) the anatomy of *L. radiata radiata* agrees "in all essential respects" with that of *L. r. siliquoidea* (Barnes). The glochidia are suboval, without hooks, and measure 0.22 to 0.23 mm in length and 0.27 to 0.28 mm in height. The host fish is unknown.

Breeding season. Ortmann (1919: 293) indicates that the breeding season begins in August and ends the following August.

Habitat. Lives in rivers and lakes of all sizes, usually in gravel or sand, occasionally in mud. Prefers tidewaters, but ascends some of the larger rivers, such as the Susquehanna River, Pennsylvania, and the Hudson River, New York, for a considerable distance.

Remarks. In the Southern Atlantic Slope region *Lampsilis radiata radiata* (Gmelin) is replaced by *Lampsilis splendida* (Lea) below the Pedee River system. But the two species do not much resemble one another, as *splendida* has a sharp posterior ridge and *r. radiata* does not. See: *Remarks* under *splendida* on p. 394. *Lampsilis r. radiata*, an Atlantic Slope species, most closely resembles *Lampsilis radiata siliquoidea* (Barnes) which is found throughout the Interior Basin. Clarke and Berg (1959: 58–62, 68–70) have shown that in the Lower St. Lawrence drainage of New York where these two otherwise quite distinct "species" commingle, they intergrade completely.

Typically, *L. r. radiata* is easily distinguished from *L. r. siliquoidea.* The former is more compressed; the difference between the male and female shell is much less marked; the periostracum is always rough and not shiny like that of *siliquoidea.* It has broader rays and often has a reddish or salmon nacre. In *siliquoidea* the nacre is always bluish white.

Ortmann (1919: 296) *suggested* for the type locality of *r. radiata* Saratoga Lake in New York, "should there not be any earlier record," and was probably unaware that Simpson (1914, 1: 65) had already selected Virginia as the type locality.

Ortmann and Walker (1922: 61) have shown that *Unio luteolus* Lamarck is not recognizable on the basis of the original description. Wheeler (1963: 58) has tried to resurrect this name on the basis of the identification of the type. Lamarck originally gave two localities, the Susquehanna and the Mohawk rivers. The former has only *L. r. radiata*, and the latter, which is now in the region of hybridization, probably did not have *L. r. siliquoidea* in it before the completion of the Erie Canal, some years after Lamarck's specimen was collected. Therefore, to avoid further confusion the type locality was restricted to the Susquehanna. See: synonymy above.

Simpson (1914, 1: 66) treats *Unio conspicuus* Lea as a variety of *Lampsilis r. radiata*, stating that "there are intermediates, which seem to fully connect the two." I am in agreement with him. The main difference in the southern specimens seems to be a general tendency to grow large more consistently than elsewhere. There

does seem to be a hiatus for this species between the Neuse River, North Carolina, and the Potomac River, Virginia. Ortmann (1919: 296) calls attention to the fact that while this species is abundant in the tidewater region of the Potomac River, it does not go up the river into the mountains west of the Blue Ridge, and is rare or absent on the Piedmont Plateau.

Range. Southern Atlantic Slope: discontinuous, Pedee River system, South Carolina, Cape Fear and Neuse river systems, *both* North Carolina. Northern Atlantic Slope: Potomac River, Maryland, north to the St. Lawrence River system, westward to Lake Ontario.

Specimens Examined

Pedee River System

Yadkin River Drainage. *North Carolina:* [Yadkin River], Salem, Forsyth Co. (MZUM). Yadkin River, near Salisbury, Rowan Co. (MZUM).

Cape Fear River System

Cape Fear River Drainage. *North Carolina:* Greenfield Pond, Wilmington, New Hanover Co. (USNM).

Neuse River System

Neuse River Drainage. *North Carolina*: Lake Michie [an impoundment on Flat River], 12 mi. NNE Durham Center, Durham Co. (75).

Potomac River System

Potomac River Drainage. *Virginia*: Potomac River, Great Falls, Fairfax Co. *District of Columbia:* Potomac River. *Virginia:* Mount Vernon, Fairfax Co.

Lampsilis (Lampsilis) splendida (Lea)
Plate 22: 4, 5

Unio splendidus Lea 1838, Trans. Amer. Philos. Soc., 6: 70, pl. 19, fig. 61 (Altamaha River, near Darien [McIntosh Co.]; Altamaha [River], Liberty [now Long] Co.; *both* Georgia; figured holotype USNM 84893). Lea, 1838, Obs. Unio, 2: 70.

Unio regularis Sowerby 1866, Conch. Iconica, 16, *Unio*, pl. 34, fig. 181, *non* Lea 1841.

Lampsilis splendida Lea. Simpson, 1914, Cat. Naiades, 1: 50.

Description. Shell large, often exceeding 110 mm in length. Outline obovate and elongated, the female proportionally higher than the male. Valves considerably inflated, subsolid. Anterior end rounded; posterior end of the male broader and very bluntly pointed; the female even more broadly rounded. Ventral margin usually slightly curved, or slightly arcuate in males when they are swollen behind the middle of the base. Dorsal margin straight, sometimes forming a distinct angle with the obliquely descending posterior margin or merging gradually into it. Hinge ligament prominent, running under the umbos and appearing anteriorly. Posterior ridge rather sharp, generally with a second ridge above it. Posterior slope considerably wrinkled. Umbos very high and full, their sculpture consisting of a number of strong, nearly straight bars. Surface of the disk sometimes smooth, but the periostracum is usually concentrically wrinkled, especially posteriorly and toward the margins. Periostracum yellowish green to brownish with the entire surface covered with numerous wide and narrow green rays. Old shells sometimes dark brown with the rays obscured.

Left valve with two compressed pseudocardinal teeth slightly anterior of the umbos, one in front of the other, the anterior one somewhat triangular; the hinder one considerably lower. Hinge line very narrow, before two short, curved, lateral teeth. Right valve with two triangular, narrow, parallel pseudocardinals separated by a deep narrow pit, the more anterior tooth inclined to be vestigial; the hinder tooth inclined to be chunky in old specimens. One rather high lateral tooth present. Beak cavities deep and wide, with dorsal muscle scars. Anterior adductor muscle scars well impressed, posterior ones less so. Pallial line distinct. Nacre white, orange,

violet, sometimes bluish, but more inclined to be pinkish and iridescent.

Length mm	Height mm	Width mm	
112	68	54	Ocmulgee River, 1 mi. S Lumber City, Telfair Co., Georgia. Female.
113	62	59	As above. Male.
73	46	36	As above. Female.
70	42	33	As above. Male.

Anatomy. Discussed by Lea (1863: 414).

Habitat. Usually lives in the swift waters of large rivers on sand bars and gravelly bottoms, but also lives in lakes.

Remarks. Lampsilis splendida (Lea) does not closely resemble any of the *Lampsilis* in either the Apalachicolan or Atlantic Slope regions. It replaces *Lampsilis radiata radiata* (Gmelin) in the Atlantic Slope region below the Pedee River system, South Carolina. *L. splendida* resembles *L. r. radiata* in its tendency to have rays which cover the entire shell, but *r. radiata* does not have a posterior ridge, while *splendida* often has quite an angular one. In *splendida* the shell of the female is proportionally higher than that of the male and more blunt behind, while in *radiata* the main difference in the shell is a tendency for the female to be expanded in the postbasal region. Young specimens of *L. ochracea* (Say) can be confused with *splendida* when the former are rayed over the entire surface, but the rays of *splendida* are narrow and wide, while those of *ochracea* are rather uniformly narrow. *L. splendida* has a much heavier shell and even in immatures the shell is heavier than the shells of *ochracea* of corresponding size.

Range. Southern Atlantic Slope: Altamaha River system, Georgia, north to the Cooper-Santee River system, South Carolina.

Specimens Examined

Altamaha River System

Ocmulgee River Drainage. *Georgia*: Limestone Creek, Brumbys Mill, 4 mi. NE Hawkinsville; Ocmulgee River, Hawkinsville; Mosquito Creek, 8 mi. SE Hawkinsville; *all* Pulaski Co. Dicksons Creek, 10 mi. NE Fitzgerald; House Creek, Bowens Mill, 9 mi. N Fitzgerald; *both* Ben Hill Co. Ocmulgee River, Jacksonville; Ocmulgee River, 1 mi. S Lumber City; *both* Telfair Co.

Oconee River Drainage. *Georgia*: Oconee River, 2.5 mi. N Glenwood, Wheeler Co.

Altamaha River Drainage. *Georgia*: Altamaha River, 7 mi. N Glenwood, Wheeler Co. Altamaha River, 10 mi. NE Surrency, Appling Co. Altamaha River, "Riverside Park," 4 mi. N Jesup, Wayne Co. Altamaha River, 3 mi. NW Everett City, Glynn Co. Altamaha River, Fort Barrington; Altamaha River, Hopeton, near Darien; *both* McIntosh Co.

Ogeechee River System

Ogeechee River Drainage. *Georgia*: Reported by Simpson (1914: 51) but the specimens were not located in the USNM.

Savannah River System

Savannah River Drainage. *Georgia*: Savannah River, 0.75 mi. SE Augusta, Richmond Co. *South Carolina:* Savannah River, 2 mi. SW Millettville; Savannah River, Johnsons Landing, 10 mi. W Allendale; Savannah River, Kingjaw Point, 10 mi. WSW Allendale; *all* Allendale Co. (*all* ANSP). *Georgia:* Savannah River, 7.5 mi. NE Shell Bluff; Savannah River, 6 mi. NE Girard; *both* Burke Co.

Cooper-Santee River System

Wateree River Drainage. *South Carolina:* Wateree River, 2.5 mi. W Camden, Kershaw Co.

Santee River Drainage. *South Carolina*: Lake Moultrie, Cross; Santee River, 1 mi. N Moncks Corner; Bunnon Lake [not located], near Alvin (ANSP and USNM); *all* Berkeley Co.

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INDEX TO RELEVANT TAXA

Principal references in boldface type.

PLATE 1

The Southeastern United States

A.M. The solid line indicates the limit of the Appalachian Mountains. The divide is somewhat to the west of it.

P.P. Piedmont Plateau. The line thus indicated, – – – – –, is the Fall Line.

C.P. Coastal Plain. The line thus indicated, · – · – ·, is the limit of the Brandywine (maximum) interglacial (now thought to be Upper Miocene) flooding, and is, in part, conjectural.

A. Area of stream capture of the New River and the North Fork of the Roanoke River.

B. Area of confluence of the headwaters of the Alabama-Coosa, Apalachicola and Savannah River systems.

C. Area of suspected stream confluence between Uphauppee Creek of the Alabama-Coosa River system and Uchee Creek of the Apalachicola River system.

D. Area of suspected confluence of the headwaters of the Choctawhatchee River and the Chattahoochee River.

The Principal Drainage Systems

1. ALABAMA-COOSA RIVER SYSTEM
    2. Coosa River Drainage
    3. Tallapoosa River Drainage

Apalachicolan Region

4. ESCAMBIA RIVER SYSTEM
5. YELLOW RIVER SYSTEM
6. CHOCTAWHATCHEE RIVER SYSTEM
7. APALACHICOLA RIVER SYSTEM
    8. Chattahoochee River Drainage
    9. Flint River Drainage
10. OCHLOCKONEE RIVER SYSTEM
11. ECONFINA RIVER SYSTEM
12. SUWANNEE RIVER SYSTEM
13. ST. MARYS RIVER SYSTEM
14. SATILLA RIVER SYSTEM

Southern Atlantic Slope Region

15. ALTAMAHA RIVER SYSTEM
    16. Ocmulgee River Drainage
    17. Oconee River Drainage
18. OGEECHEE RIVER SYSTEM
19. SAVANNAH RIVER SYSTEM
20. EDISTO RIVER SYSTEM
21. COOPER-SANTEE RIVER SYSTEM
    22. Saluda River Drainage
    23. Broad River Drainage
    24. Catawba River Drainage
25. BLACK RIVER SYSTEM
26. PEDEE RIVER SYSTEM
    27. Yadkin River Drainage
28. WACCAMAW RIVER SYSTEM
29. CAPE FEAR RIVER SYSTEM
30. NEUSE RIVER SYSTEM
31. PAMLICO RIVER SYSTEM
32. ROANOKE RIVER SYSTEM
    33. Dan River Drainage
    34. Roanoke River Drainage
35. CHOWAN RIVER SYSTEM
36. JAMES RIVER SYSTEM

Northern Atlantic Slope Region

37. YORK RIVER SYSTEM
38. RAPPAHANNOCK RIVER SYSTEM
39. POTOMAC RIVER SYSTEM
    40. Shenandoah River Drainage


SOUTHEASTERN UNITED STATES
VA.
N. C.
S. C.
GA.
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PLATE 2

Pleurobema (Lexingtonia) collina (Conrad)

Fig. 1. *Unio collinus* Conrad. North [= Maury] River, a branch of the James River [Rockbridge County], Virginia. Lectotype ANSP 41007. Length 46 mm, height 30 mm, width 19 mm (nat. size).

Fig. 2. [James River] USNM 84376. Length 18.8 mm. Specimen sprayed with ammonium chloride vapor. After Boss and Clench (1967, pl. 15, fig. 2).

Pleurobema (Lexingtonia) masoni (Conrad)

Fig. 3. *Unio masoni* Conrad. Savannah River, Augusta [Richmond County], Georgia. Holotype ANSP 41333. Length 26.6 mm, height 19.3 mm, width 13.3 mm (nat. size).

Fig. 4. Mill Race, 2 mi. N of Sardis, Burke County, Georgia, MCZ 234387. Length 47 mm, height 28 mm, width 19 mm (nat. size).

Fig. 5. *Unio masoni* Conrad. Savannah River, Augusta [Richmond County], Georgia. Paratype ANSP 41332. Length 37 mm, height 26 mm, width 16 mm (nat. size).

Fig. 6. *Unio castus* Lea. South Carolina. Holotype USNM 84782. Length 40 mm, height 27 mm, width 17 mm (nat. size).

Fig. 7. *Unio brimleyi* Wright. [Walnut Creek of] Neuse River, Raleigh [Wake County], North Carolina. Lectotype USNM 149651. Length 38 mm, height 29 mm, width 15 mm (nat. size).

Fig. 8. *Unio merus* Lea. Abbeville District [Savannah River drainage], South Carolina. Holotype USNM 85698. Length 38 mm, height 29 mm, width 15 mm (nat. size).

Fig. 9. *Unio pumilus* Lea. Black River [about 10 mi. W of Benson, Johnston County], North Carolina. Holotype USNM 84545. Length 28 mm, height 20 mm, width 13 mm (nat. size).

Fig. 10. *Unio striatulus* Lea. Roanoke River, Weldon [Halifax County], North Carolina. Holotype USNM 84548. Length 39 mm, height 28 mm, width 17 mm (nat. size).

Elliptio (Canthyria) spinosa (Lea)

Fig. 11. Altamaha River, 4 mi. NE of Jesup, Wayne County, Georgia. MCZ 234055. Length 59 mm, height 37 mm, width 22 mm (approximately 1.2 ×).

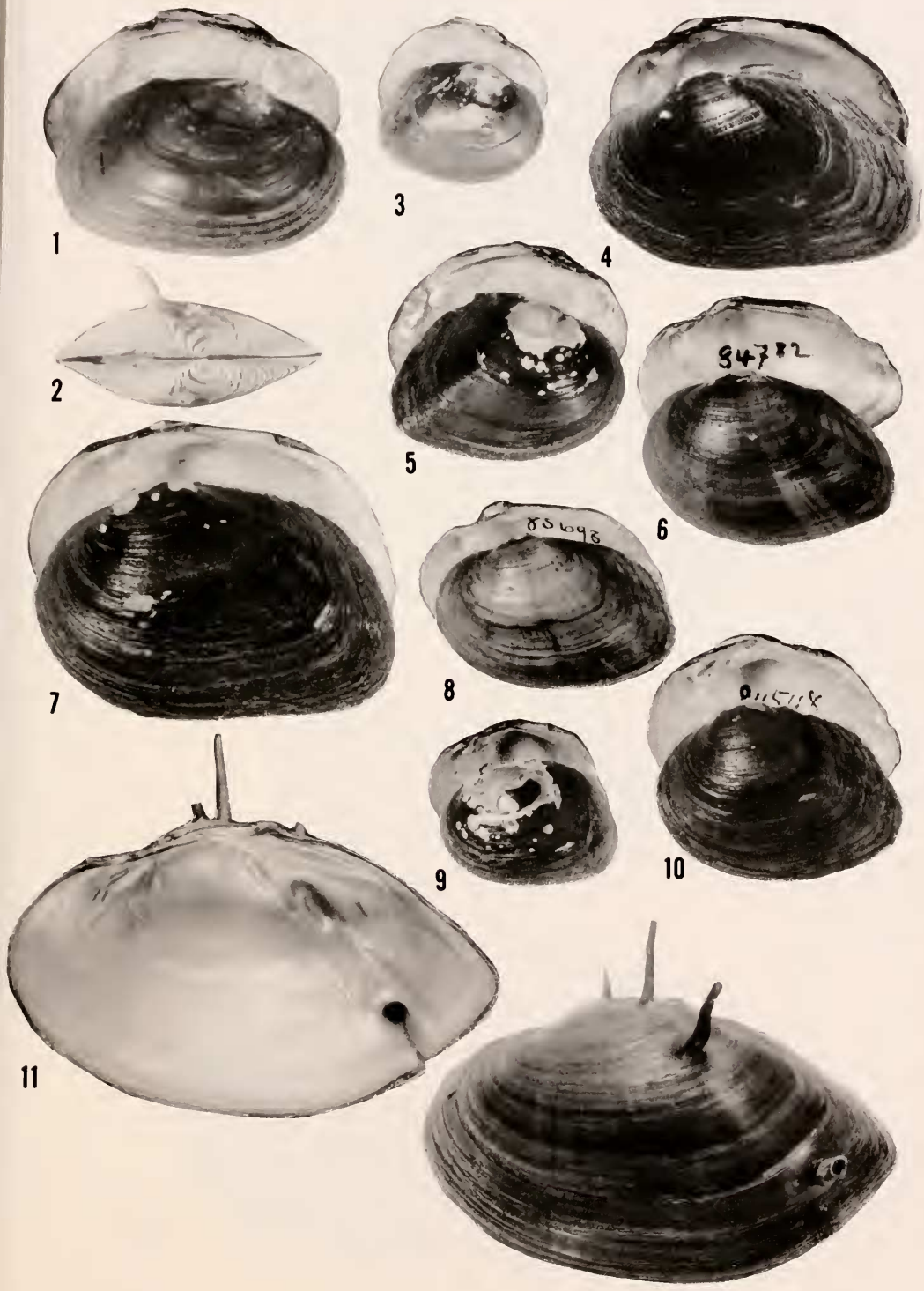
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PLATE 3

Elliptio (Elliptio) crassidens crassidens (Lamarck)

Fig. 1. *Unio lehmanii* Wright. St. Marys River [Nassau County], Florida. Lectotype USNM 149650. Length 60 mm, height 40 mm, width 24 mm (nat. size).

Fig. 2. *Unio polymarphus* Wright. Spanish Creek [a tributary of the St. Marys River W of Folkston], Charleton County, Georgia. Lectotype USNM 152060. Length 75 mm, height 46 mm, width 29 mm (slightly reduced).

Fig. 3. Spanish Creek, Charleton County, Georgia. MCZ 269228. Length 62 mm, height 40 mm, width 30 mm (slightly reduced).

Fig. 4. As above. Length 94 mm, height 57 mm, width 38 mm (slightly reduced).

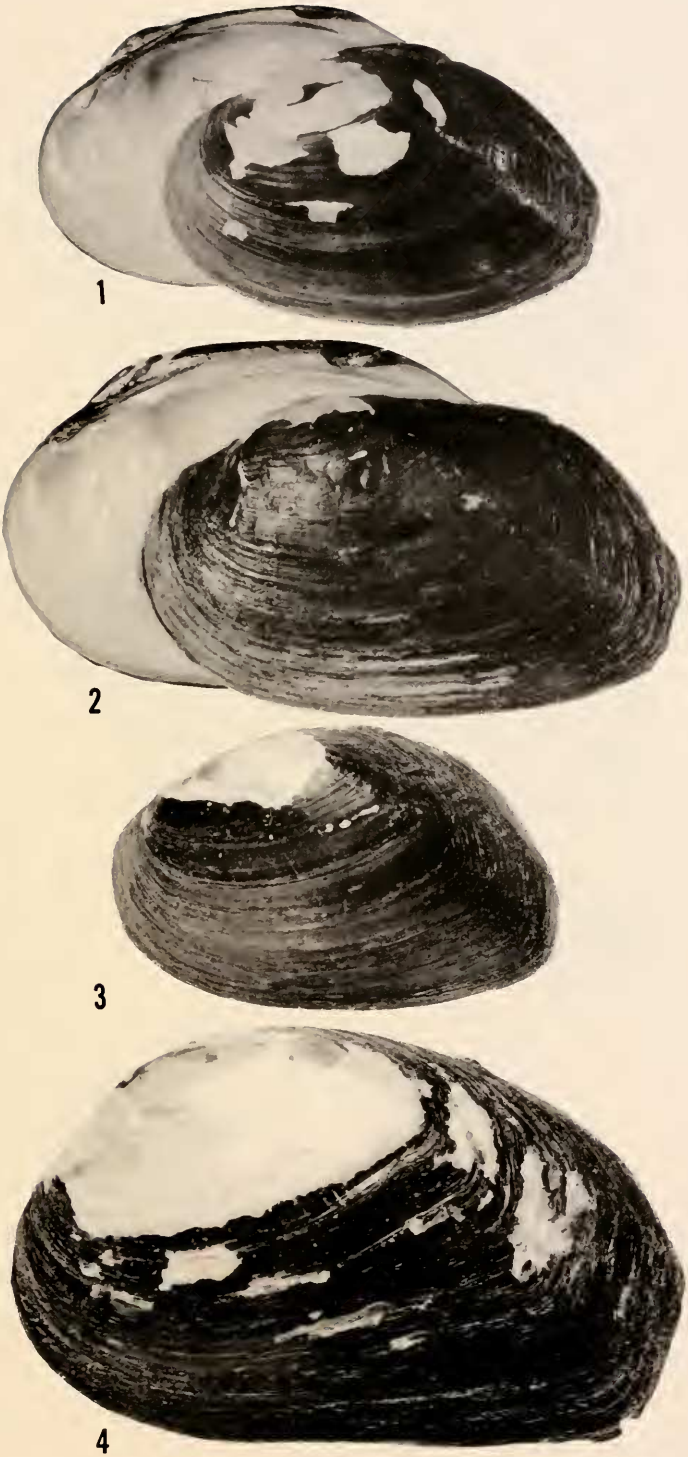
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PLATE 4

Elliptio (*Elliptio*) *crassidens downiei* (Lea)

Fig. 1. *Unio downiei* Lea. Buck Lake, a bayou of the Satilla River, Wayne [Brantly] County, Georgia. Holotype USNM 84854. Length 84 mm, height 49 mm, width 36 mm (slightly reduced).

Fig. 2. *Unio satillaensis* Lea. Satilla River, Camden County, Georgia. Holotype USNM 84855. Length 75 mm, height 45 mm, width 30 mm (slightly reduced).

Fig. 3. Satilla River, 3 mi. S of Hortense, Brantly County, Georgia. MCZ 237460. Length 27 mm, height 16 mm, width 8 mm (nat. size).

Fig. 4. *Unio spissus* Lea. Satilla River, Wayne County, Georgia. Holotype USNM 84853. Length 76 mm, height 57 mm, width 40 mm (approximately nat. size).

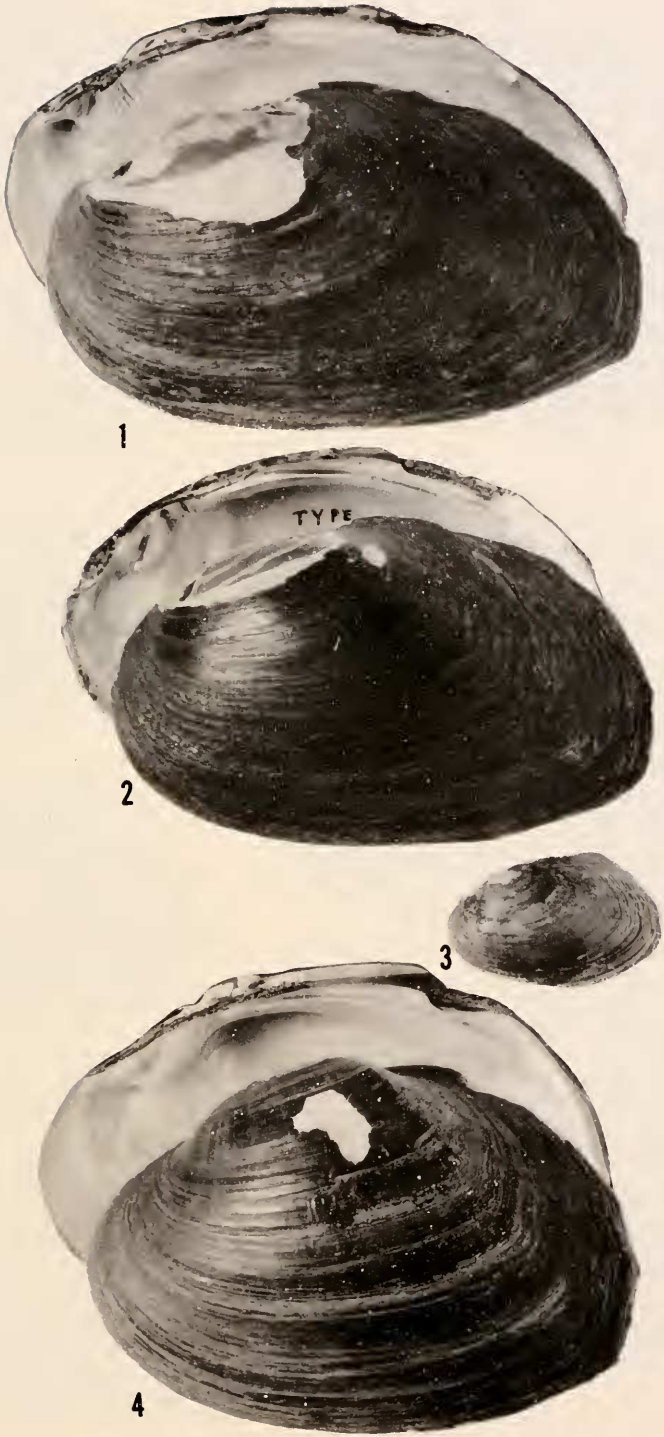
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PLATE 5

Elliptio (Elliptio) congaraea (Lea)

Fig. 1. *Unio congaraeus* Lea. Congaree River [Cooper-Santee River system], South Carolina. Holotype USNM 85693. Length 41 mm, height 25 mm, width 14 mm (slightly reduced).

Fig. 2. *Unio fulvus* Lea. South Carolina. Holotype USNM 85679. Length 40 mm, height 21 mm, width 15 mm (slightly reduced).

Fig. 3. *Unio vestitus* Lea. Ogeechee River [Georgia]. Holotype USNM 85332. Length 39 mm, height 25 mm, width 15 mm (nat. size).

Fig. 4. *Unio forbesianus* Lea. Savannah River, Georgia. Holotype USNM 84542. Length 45 mm, height 31 mm, width 29 mm (nat. size).

Fig. 5. *Unio lecontianus* Lea. Canoochee River, Liberty County, Georgia. Holotype USNM 84852. Length 70 mm, height 45 mm, width 29 mm (slightly reduced).

Fig. 6. *Unio dorsatus* Lea. Catawba River, North Carolina. Holotype USNM 84494. Length 57 mm, height 40 mm, width 23 mm (nat. size).

Fig. 7. *Unio moussanianus* Lea. Georgia. Holotype USNM 85168. Length 72 mm, height 49 mm, width 28 mm (slightly reduced).

Fig. 8. *Unio carvus* Lea. Buckhead Creek, Burke County, Georgia. Holotype USNM 84539. Length 62 mm, height 40 mm, width 25 mm (nat. size).

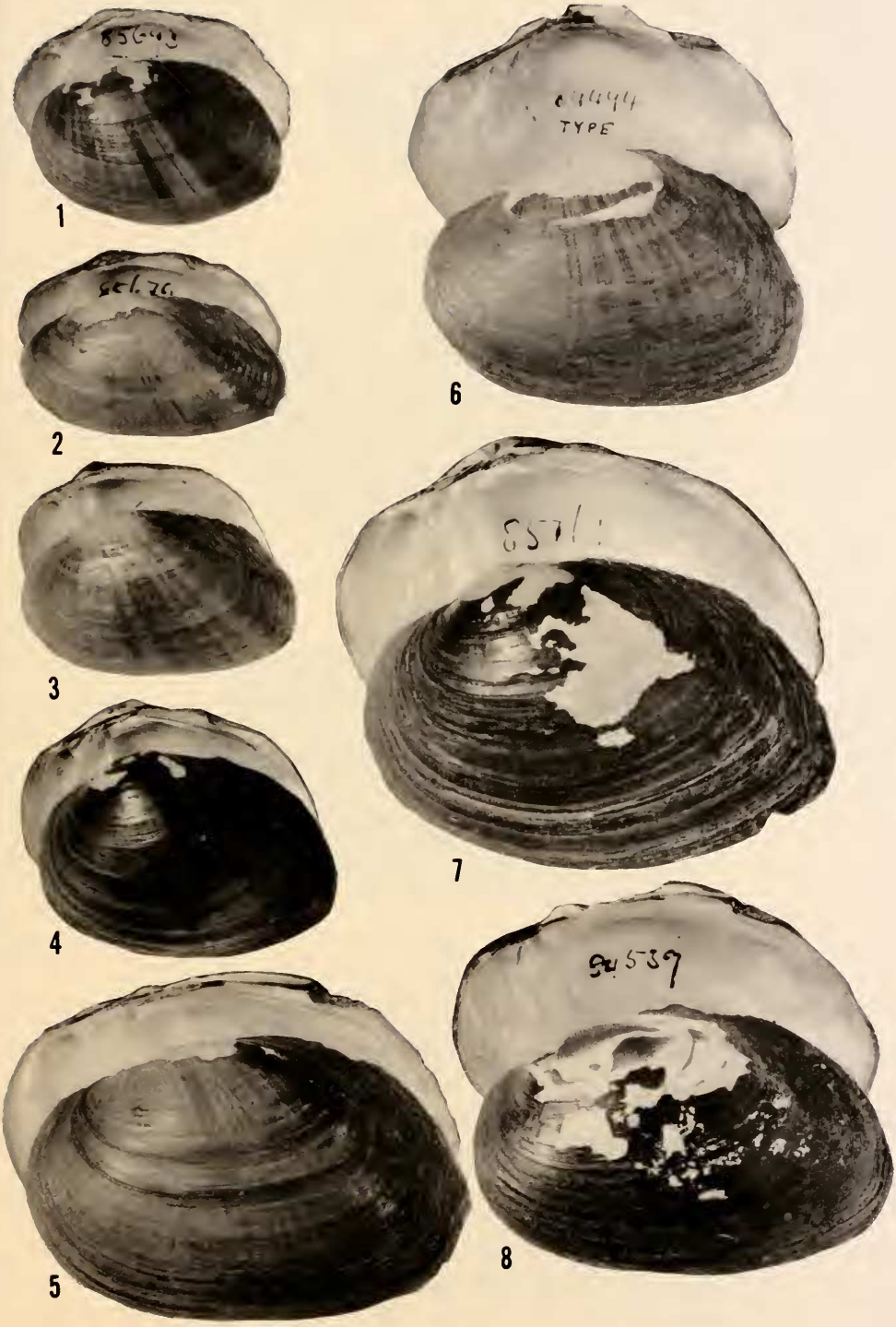
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PLATE 6

Elliptio (*Elliptio*) *dariensis* (Lea)

Fig. 1. House Creek, Bowens Mills, 9 mi. N of Fitzgerald, Ben Hill County, Georgia. MCZ 234237. Length 41 mm, height 23 mm, width 14 mm (not. size).

Fig. 2. *Unio dariensis* Lea. [Altamaha River] near Darien [McIntosh County], Georgia. Holotype USNM 85691. Length 78 mm, height 55 mm, width 28 mm (slightly reduced).

Fig. 3. House Creek, Bowens Mill, 9 mi. N of Fitzgerald, Ben Hill County, Georgia. MCZ 234237. Length 76 mm, height 45 mm, width 26 mm (not. size).

Fig. 4. As above. Length 98 mm, height 58 mm, width 35 mm (not. size).


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PLATE 7

Elliptio (*Elliptia*) *fraterna* (Lea)

Fig. 1. *Unio fraternus* Lea. Abbeville District [Savannah River drainage], South Carolina. Holotype USNM 85396. Length 60 mm, height 31 mm, width 16 mm (slightly reduced).

Fig. 2. *Unio fraternus* Lea. [Chattahoochee River] Columbus [Muscogee County], Georgia. Paratype USNM 85398. Length 69 mm, height 34 mm, width 17 mm (slightly reduced).

Fig. 3. *Unio anthonyi* Lea. Florida. Holotype USNM 84986. Length 58 mm, height 35 mm, width 22 mm (slightly reduced).

Fig. 4. Flat Creek, 8 mi. SW of Samson, Geneva County, Alabama. MCZ 186967. Length 75 mm, height 38 mm, width 20 mm.

Fig. 5. *Elliptio mcmichaeli* Clench and Turner. Choctawhatchee River, 8 mi. W of Miller Cross Roads, Holmes County, Florida. Holotype MCZ 191922. Length 91 mm, height 50 mm, width 27 mm.

Elliptio waccamawensis (Lea)

Fig. 6. *Unio waccamawensis* Lea. Lake Waccamaw, North Carolina. Holotype USNM 84437. Length 36 mm, height 17 mm, width 16 mm (nat. size).

Fig. 7. Canal beside Lake Waccamaw, 1 mi. NNW of Dupree Londing, Columbus County, North Carolina. MCZ 214235. Length 89 mm, height 45 mm, width 28 mm (approximately not. size).

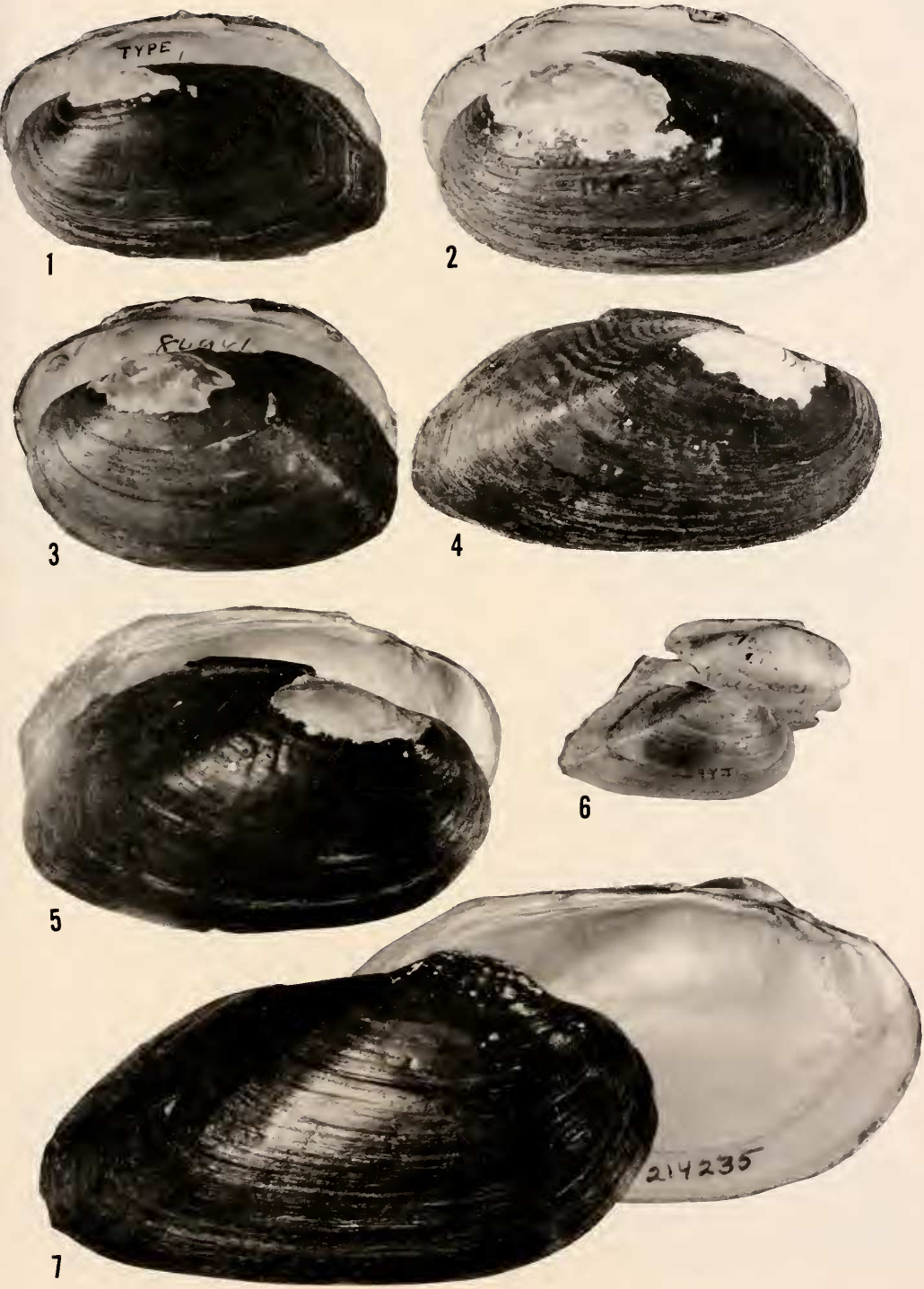
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PLATE 8

Elliptio (*Elliptio*) *complanata* (Lightfoot)

Fig. 1. Savannah River, 7 mi. NE of Newington, Screven County, Georgia. MCZ 269257. Length 99 mm, height 50 mm, width 28 mm (slightly enlarged).

Fig. 2. Turkey Creek, 4 mi. NE of Allentown [Altamaha River system], Wilkinson County, Georgia. MCZ 234355. Length 73 mm, height 36 mm, width 18 mm (nat. size).

Fig. 3. *Unio quadrilaterus* Lea. Neuse River, near [6 mi. E of] Raleigh, [Wake County], North Carolina. Holotype USNM 85385. Length 60 mm, height 36 mm, width 20 mm (slightly reduced).

Fig. 4. *Unio roanokensis* Lea. Roanoke River [road between Norfolk, Virginia, and Tarboraugh, North Carolina]. Holotype USNM 85423. Length 119 mm, height 57 mm, width 29 mm (slightly reduced).

Fig. 5. *Unio mediocris* Lea. Neuse River, [6 mi. E of] Raleigh [Wake County], North Carolina. Holotype USNM 85611. Length 57 mm, height 30 mm, width 19 mm (slightly reduced).

Fig. 6. North shore, Lake Waccamaw, town of Lake Waccamaw, Columbus County, North Carolina. MCZ 258813. Length 60 mm, height 31 mm, width 18 mm (approximately nat. size).

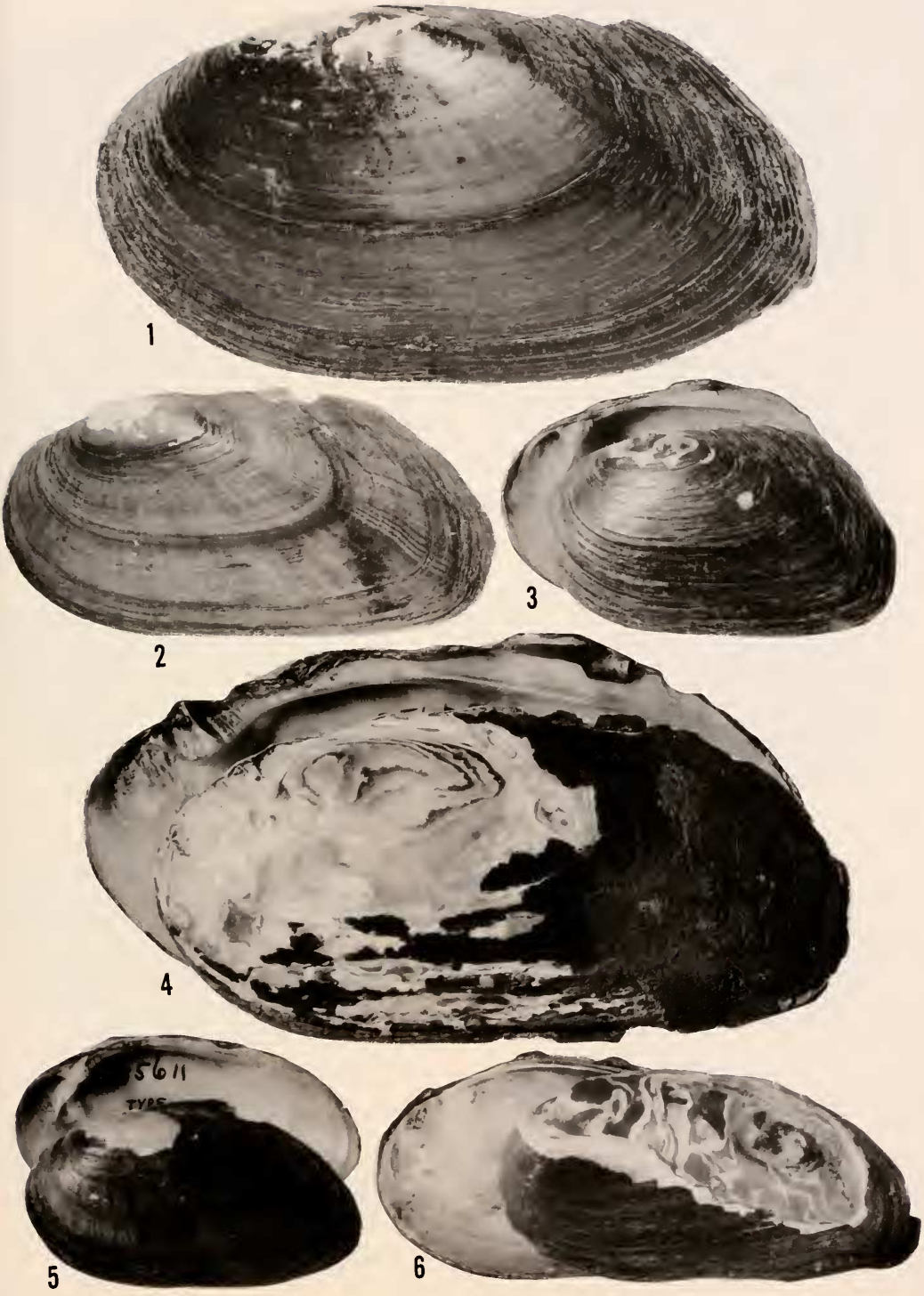
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PLATE 9

Elliptio (Elliptio) hapetanensis (Lea)

Fig. 1. *Unio inusitatis* Lea. Swift Creek, below Macon [Bibb County], Georgia. Holotype USNM 85531. Length 57 mm, height 32 mm, width 19 mm (slightly reduced).

Fig. 2. *Unio hapetanensis* Lea. [Altamaha River], Hapetan, near Darien [McIntash County], Georgia. Holotype USNM 85391. Length 84 mm, height 43 mm, width 20 mm (slightly reduced).

Elliptio (Elliptio) icterina (Conrad)

Fig. 3. *Unio icterinus* Conrad. Savannah River, opposite Augusta [Richmond County], Georgia. Holotype ANSP 41381. Length 55 mm, height 28 mm, width 18 mm (approximately nat. size).

Fig. 4. *Unio lugubris* Lea. [Altamaha River], Hapetan, near Darien [McIntash County], Georgia. Holotype USNM 85638. Length 53 mm, height 37 mm, width 22 mm (slightly enlarged).

Fig. 5. *Unio tuomeyi* Lea. Abbeville District [Savannah River drainage]. South Carolina. Holotype USNM 85669. Length 65 mm, height 33 mm, width 19 mm (slightly reduced).

Fig. 6. *Unio opacus* Lea. Buckhead Creek, Burke County, Georgia. Holotype USNM 85546. Length 66 mm, height 37 mm, width 24 mm (slightly reduced).

Fig. 7. *Unio hastatus* Lea. New Market, Abbeville District [Savannah River drainage], South Carolina. Holotype USNM 86013. Length 66 mm, height 28 mm, width 17 mm (slightly reduced).

Fig. 8. *Unio abnubilus* Lea. Buckhead Creek, Burke County, Georgia. Holotype USNM 85646. Length 65 mm, height 38 mm, width 23 mm (slightly reduced).

Fig. 9. *Unio similis* Lea. Buckhead Creek, Burke County, Georgia. Holotype USNM 85653. Length 57 mm, height 31 mm, width 20 mm (slightly reduced).

Fig. 10. *Unio aequatus* Lea. Buckhead Creek, Burke County, Georgia. Holotype USNM 85561. Length 66 mm, height 38 mm, width 21 mm (slightly reduced).

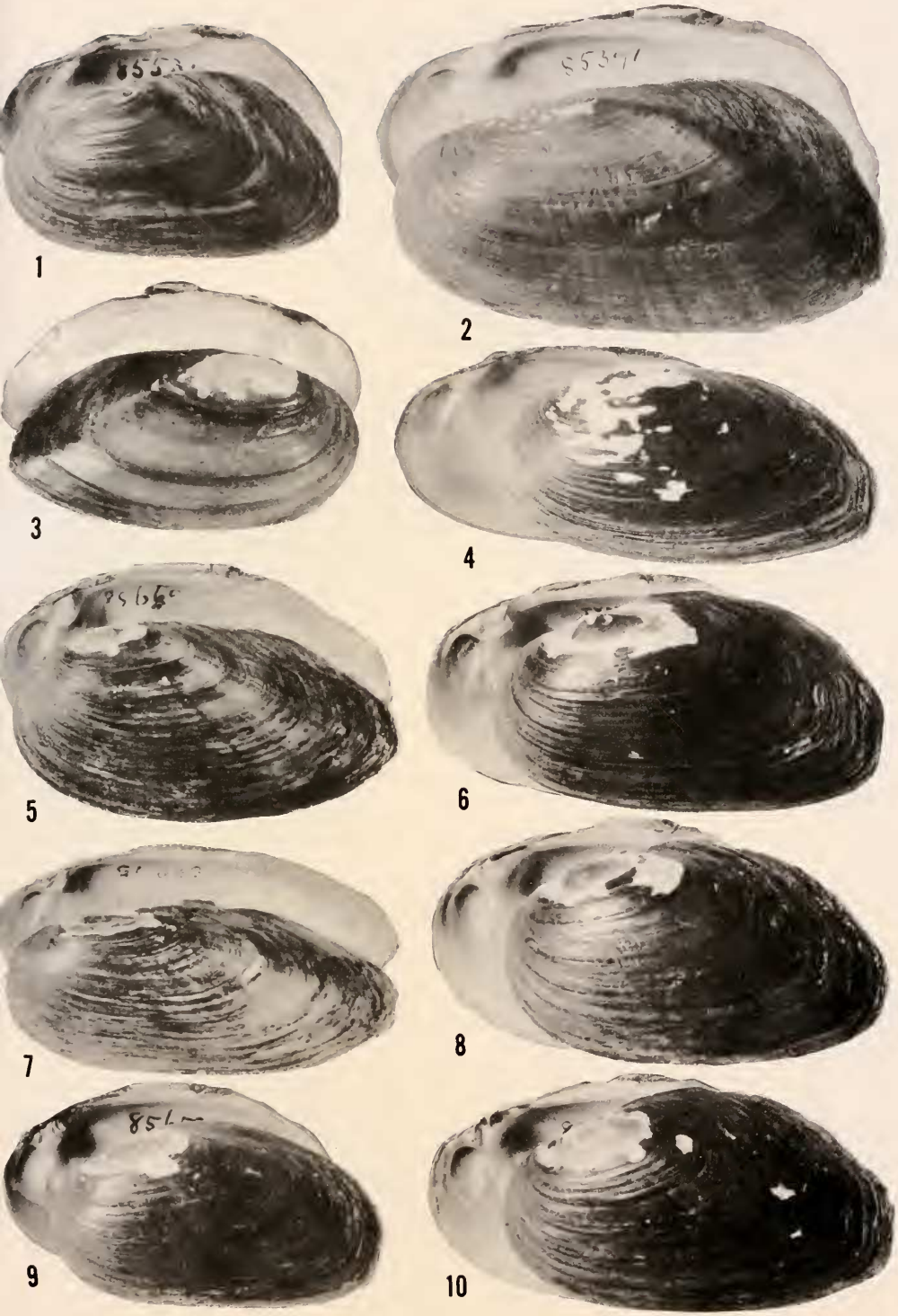
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PLATE 10

Elliptio (*Elliptio*) *icterina* (Conrad)

Fig. 1. *Unio micans* Lea. Catawba River, Gaston County, North Carolina. Holotype USNM 85077. Length 44 mm, height 23 mm, width 14 mm (slightly reduced).

Fig. 2. *Unio ocmulgéensis* Lea. Little Ocmulgee River, Lumber City, [Telfair County], Georgia. Holotype USNM 85901. Length 104 mm, height 50 mm, width 35 mm (slightly reduced).

Fig. 3. *Unio confertus* Lea. Santee Canal, South Carolina, from J. Lewis. Metotype USNM 85634. Length 60 mm, height 33 mm, width 22 mm (slightly reduced).

The holotype was not located. This specimen, identified by Lea, is almost the same width and height as the original specimen, though the latter was more inflated, measuring 28 mm in width.

Elliptio (*Elliptio*) *arctata* (Conrad)

Fig. 4. *Unio arctatus* Conrad. Alabama River, Alabama. Lectotype ANSP 41356. Length 55 mm, height 22 mm, width 14 mm (nat. size).

Fig. 5. *Unio strigosus* Lea. Chattahoachee River, Columbus [Muscogee County], Georgia. Holotype USNM 85890. Length 56 mm, width 24 mm, height 13 mm (slightly reduced).

Fig. 6. *Unio lazarus* Lea. Abbeville District [Savannah River drainage], South Carolina. Holotype USNM 86155. Length 52 mm, height 23 mm, width 12 mm (slightly reduced).

Fig. 7. *Unio perstriatus* Lea. Abbeville District [Savannah River drainage], South Carolina. Holotype USNM 85892. Length 57 mm, height 25 mm, width 12 mm (slightly reduced).

Fig. 8. *Unio gracilentus* Lea. Catawba River, Gaston County, North Caralina. Holotype USNM 85976. Length 71 mm, height 30 mm, width 13 mm (slightly reduced).

Fig. 9. *Unio perlatus* Lea. Cape Fear River, Black Rock Landing [= 2 mi. S of Kings Bluff, Bladen County], North Carolina. Holotype USNM 86006. Length 66 mm, height 22 mm, width 12 mm (slightly reduced).

Elliptio (*Elliptio*) *lanceolata* (Lea)

Fig. 10. *Unio productus* Conrad. Savannah River, Augusta [Richmond County, Georgia]. Holotype ANSP 41397. Length 66 mm, height 26 mm, width 16.5 mm (approximately nat. size).


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PLATE 11

Elliptio (*Elliptio*) *lanceolata* (Lea)

Fig. 1. *Unio subcylindraceus* Lea. Racky Creek, near Macan [Bibb County], Georgia. Holatype USNM 85863. Length 95 mm, height 41 mm, width 36 mm (slightly reduced).

Fig. 2. *Unio lanceolatus* Lea. Tar River, Tarboraugh [Edgecombe County], North Carolina. Holotype USNM 85905. Length 41 mm, height 18 mm, width 11 mm (slightly reduced).

Fig. 3. *Unio angustatus* Lea. Cooper River, South Carolina. Holatype USNM 85896. Length 72 mm, height 29 mm, width 17 mm (slightly reduced).

Fig. 4. *Unio emmonsii* Lea. Roanoke River, Weldon [Halifax County], North Carolina. Holotype USNM 86028. Length 110 mm, height 46 mm, width 26 mm (slightly reduced).

Fig. 5. *Unio hazelhurstianus* Lea. Satilla River, Camden County, Georgia. Halotype USNM 86009. Length 78 mm, height 35 mm, width 22 mm (slightly reduced).

Fig. 6. *Unio fisherianus* Lea. Head of Chester River [Kent County], Maryland. Holotype USNM 86002. Length 70 mm, height 29 mm, width 15 mm (slightly reduced).

Elliptia (*Elliptio*) *shepardiana* (Lea)

Fig. 7. Ocmulgee River, 1 mi. S of Lumber City, Telfair Caunty, Georgia. MCZ 234042. Length 127 mm, height 29 mm, width 15 mm (slightly enlarged).

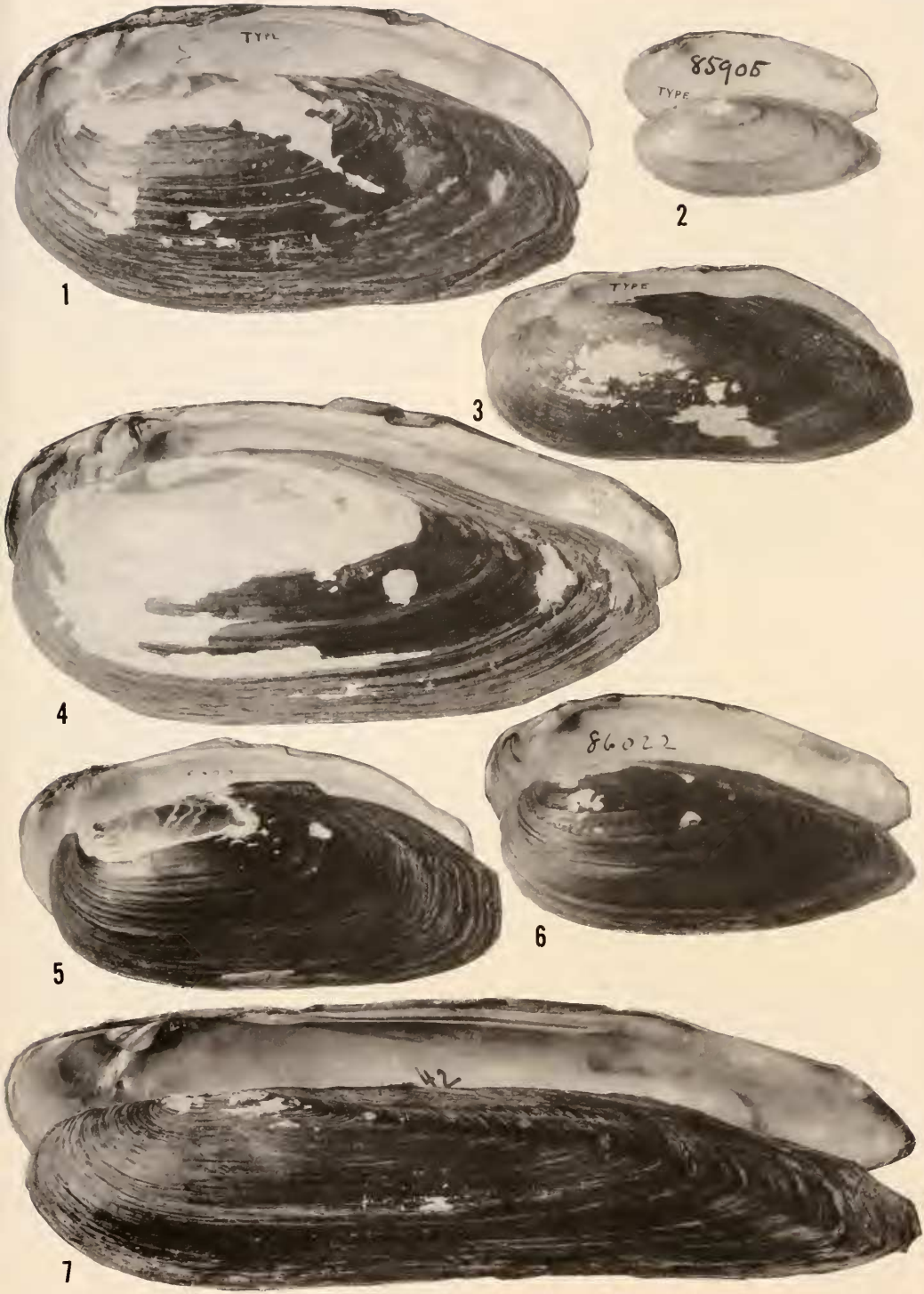
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PLATE 12

Uniamerus tetralasmus (Say)

Fig. 1. *Unio abesus* Lea. Little Ogeechee River [Hancock County], Georgia. Holotype USNM 85366. Length 82 mm, height 50 mm, width 35 mm (slightly reduced).

Fig. 2. *Unio bisselianus* Lea. Bissels Pond, Charlotte [Mecklenburg County], North Carolina. Holotype USNM 85373. Length 69 mm, height 40 mm, width 24 mm (slightly reduced).

Fig. 3. *Unio squalidus* Lea. Roanoke River, near Weldon [Halifax County], North Carolina. Holotype USNM 85376. Length 52 mm, height 30 mm, width 18 mm (slightly reduced).

Fig. 4. *Unio cicur* Lea. Little Ocmulgee River, Georgia. Holotype USNM 85532. Length 41 mm, height 25 mm, width 17 mm (slightly reduced).

Fig. 5. *Unio ineptus* Lea. Abbeville District [Savannah River drainage], South Carolina. Holotype USNM 85326. Length 33 mm, height 18 mm, width 10 mm (slightly reduced).

Fig. 6. *Unio pawensis* Lea. Beaver Creek [into ?], Catawba Run [Gaston and Mecklenburg Counties], North Carolina. Holotype USNM 85380. Length 74 mm, height 42 mm, width 29 mm (slightly reduced).

Lasmigona (*Platynaias*) *subviridis* (Conrad)

Fig. 7. *Unio pertenuis* Lea. Neuse River, near [6 mi. E of] Raleigh [Wake County], North Carolina. Holotype USNM 86139. Length 35 mm, height 22 mm, width 13 mm (slightly reduced).

Fig. 8. *Unio hyalinus* Lea. [James River drainage], Richmond [Henrico County], Virginia. Holotype USNM 86131. Length 35 mm, height 21 mm, width 12 mm (slightly reduced).

Fig. 9. *Unio charlottensis* Lea. [Sugar Creek], near Charlotte, Mecklenburg County, North Carolina. Holotype USNM 85402. Length 101 mm, height 58 mm, width 34 mm (slightly reduced).

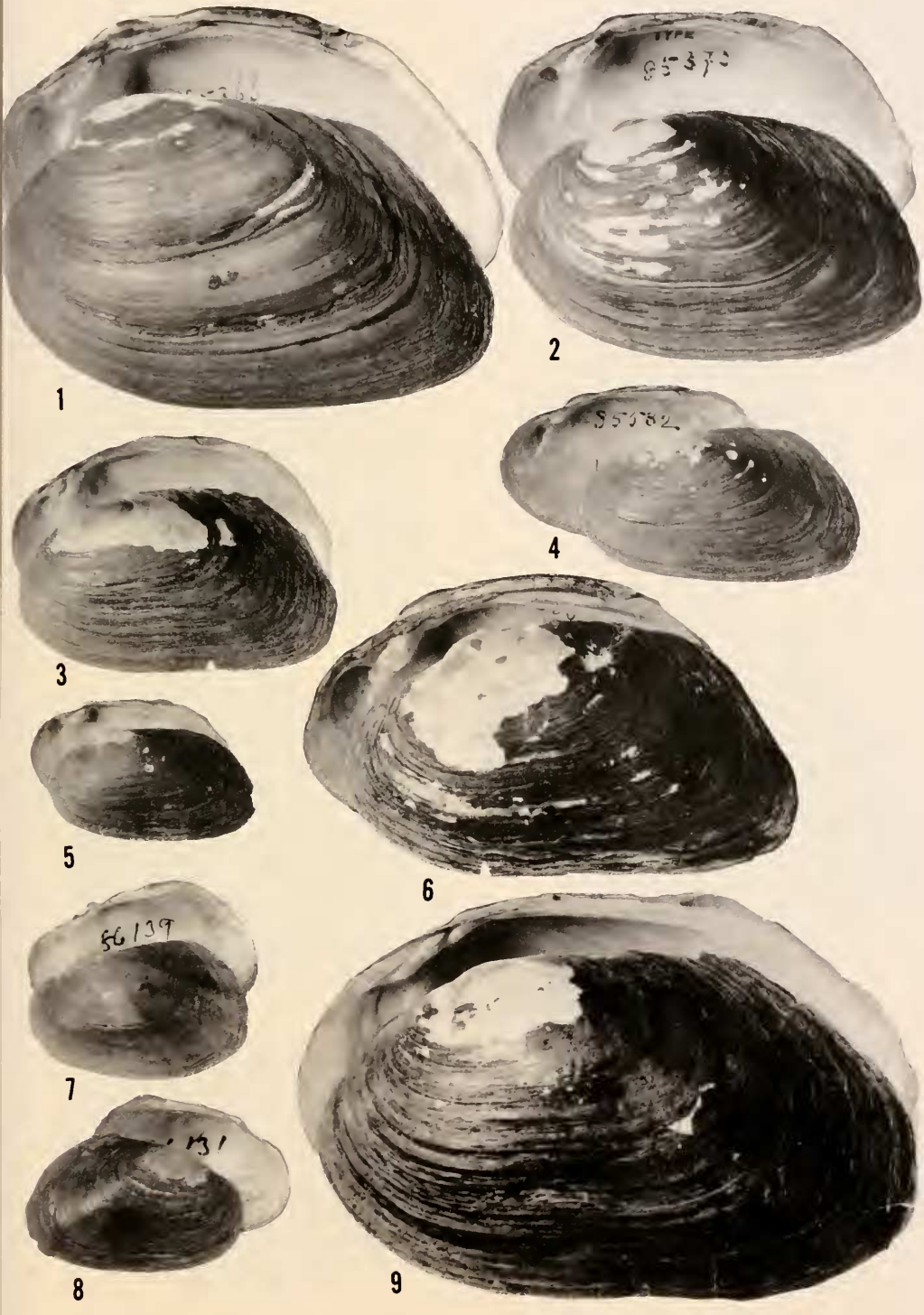
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PLATE 13

Lasmigona (*Platynaias*) *subviridis* (Conrad)

Fig. 1. *Unio decoratus* Lea. Abbeville District [Savannah River drainage], South Carolina. Holotype USNM 83972. Length 60 mm, height 37 mm, width 19 mm (slightly reduced).

Alasmidonta (*Prolasmidonta*) *heterodan* (Lea)

Fig. 2. Neuse River [6 mi. E of] Raleigh [Wake County], North Carolina. MCZ 231191. Length 34 mm, height 19 mm, width 14 mm (1.5 ×).

Alasmidonta (*Alasmidonta*) *undulata* (Say)

Fig. 3. Nottoway River, 3 mi. E of Rawlings, Brunswick County, Virginia. MCZ 237455. Length 54 mm, height 32 mm, width 23 mm (approximately nat. size).

Fig. 4. James River, opposite Maidens, Goochland County, Virginia. MCZ 261313. Length 29 mm, height 19 mm, width 13 mm (1.5 ×).

Alasmidonta (*Alasmidonta*) *triangulata* (Lea)

Fig. 5. *Margaritana triangulata* Lea. Upper Chattahoochee [River], Georgia. Holotype USNM 86249. Length 57 mm, height 38 mm, width 31 mm (nat. size).

Fig. 6. Mill Race, 2 mi. N of Sardis, Burke County, Georgia. MCZ 237453. Length 48 mm, height 32 mm, width 27 mm (slightly enlarged).

Alasmidonta (*Alasmidonta*) *arcula* (Lea)

Fig. 7. *Margaritana arcula* Lea. Altamaha [River], Liberty [now Long] County, Georgia. Holotype USNM 86170. Length 57 mm, height 44 mm, width 41 mm (nat. size).

Fig. 8. Altamaha River, 4 mi. NE of Jesup, Wayne County, Georgia. MCZ 237551. Length 50 mm, height 43 mm, width 38 mm (slightly enlarged).

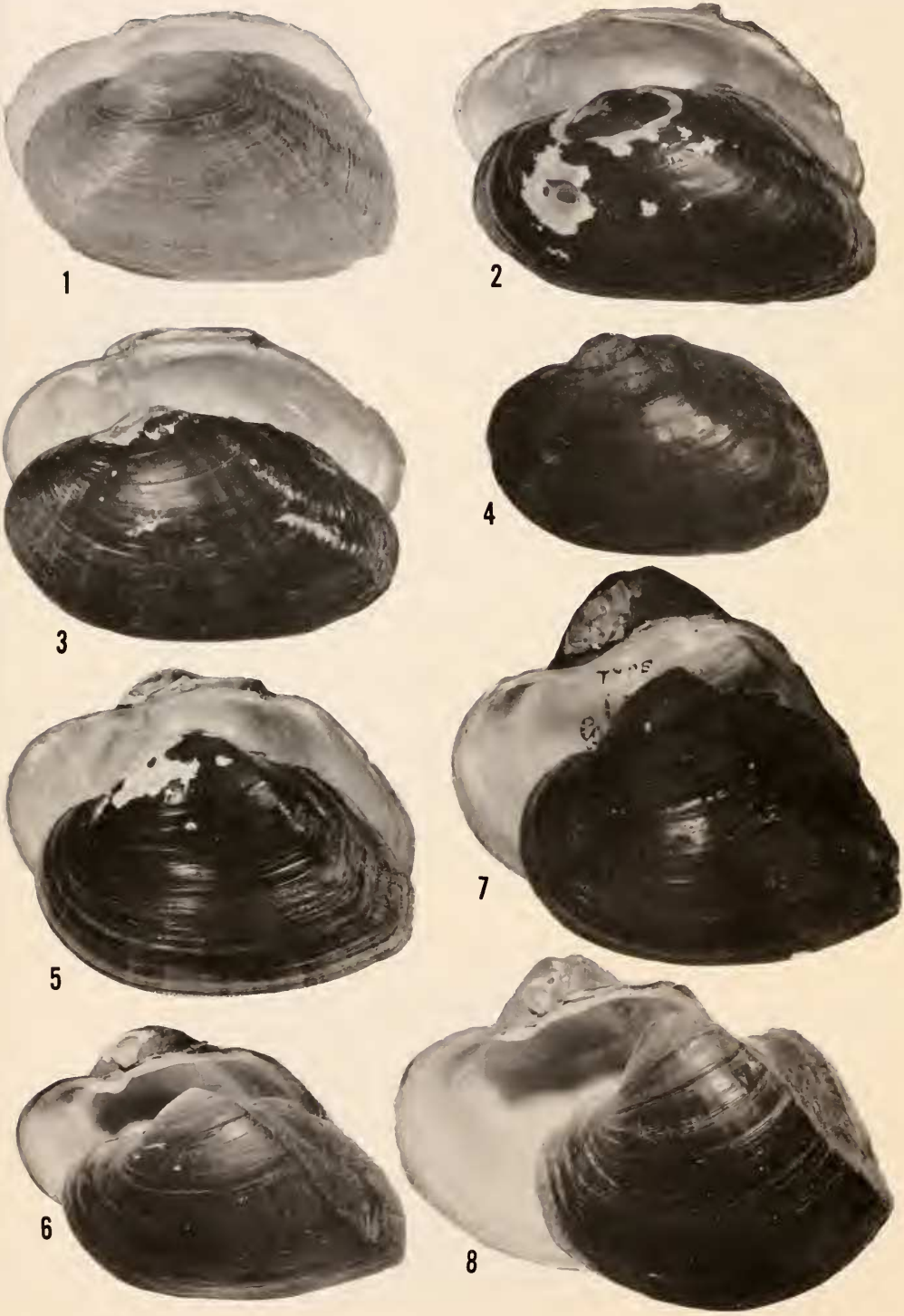
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PLATE 14

Alasmidonta (Decurambis) varicosa (Lamarck)

Fig. 1. Turkey Creek, 8 mi. NW of Edgefield, Edgefield County, South Carolina. MZUM 58024. Length 44 mm, height 26 mm, width 18 mm (slightly reduced).

Fig. 2. North Fork of Shenandoah River, E of Woodstock, Shenandoah County, Virginia. MCZ 216721. Length 45 mm, height 25 mm, width 18 mm (2×).

Anodonta (Pyganodon) cataracta cataracta Say

Fig. 3. *Anodonta daliaris* Lea. Stewarts Mill Dam, Union County, North Carolina. Topotype MZUM 103859, from the original lot collected by C. M. Wheatley. Lea saw only the holotype in the ANSP 126522a. Length 111 mm, height 67 mm, width 50 mm (slightly reduced).

Fig. 4. *Anodonta dariensis* Lea. Swift Creek, near Macon [Bibb County], Georgia. Holotype USNM 86600. Length 107 mm, height 58 mm, width 49 mm (slightly reduced).

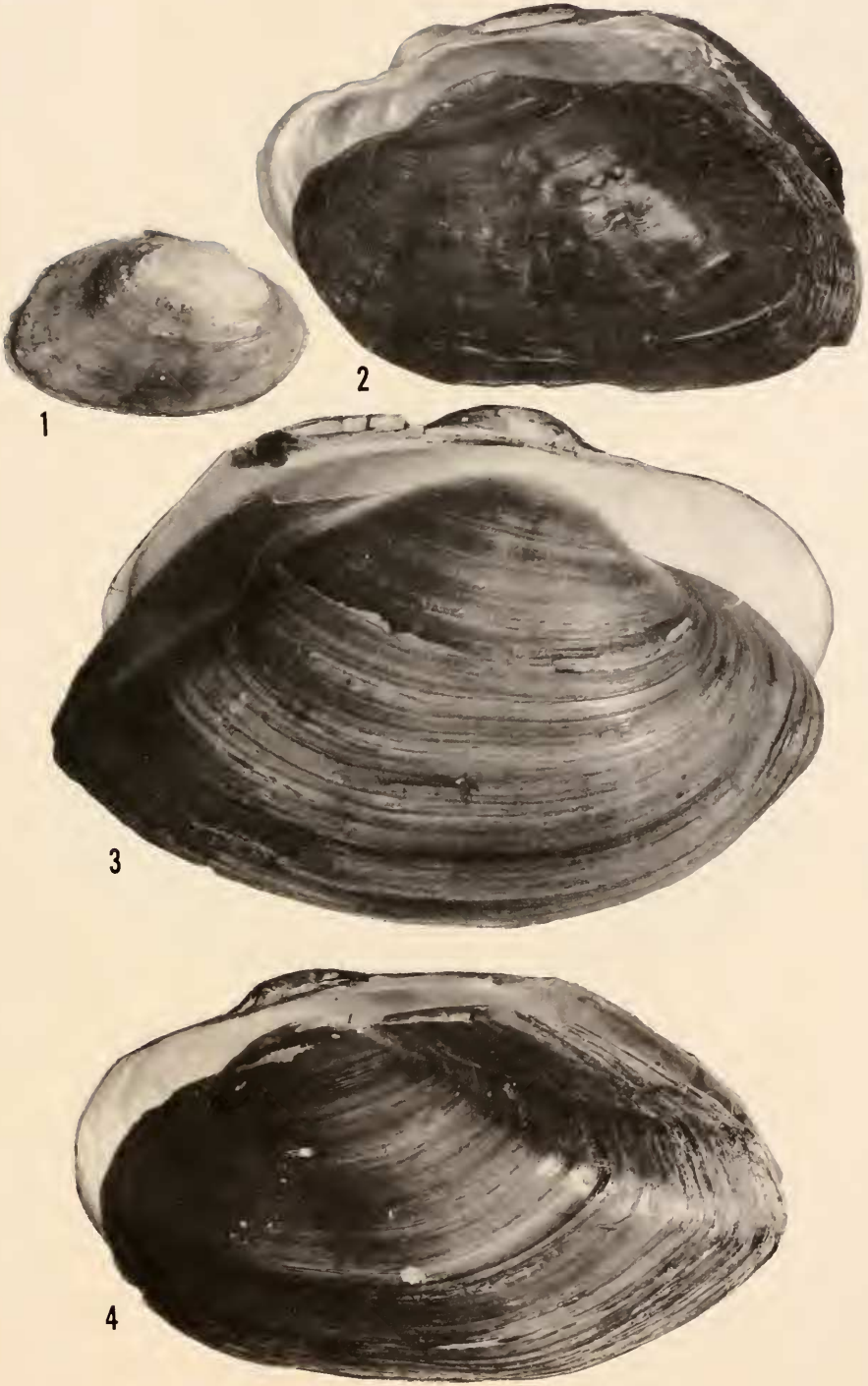
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PLATE 15

Anodonta (Pyganodon) cataracta cataracta Say

Fig. 1. *Anodonta virgulata* Lea. Roanoke River, Weldon [Halifax County], North Carolina. Holotype USNM 86593. Length 78 mm, height 44 mm, width 33 mm.

Anodonta (Pyganodon) gibbosa Say

Fig. 2. Altamaha River, "Riverside Park," 4 mi. N of Jesup, Wayne County, Georgia. MCZ 234056. Length 40 mm, height 30 mm, width 22 mm ($1\frac{3}{8}\times$).

Fig. 3. Cedar Creek, Fountains Mill, 7 mi. SW of Howkinsville, Pulaski County, Georgia. MCZ 111438. Length 107 mm, height 61 mm, width 48 mm (slightly reduced).

Anodonta (Pyganadon) implicata Say

Fig. 4. *Anodonta newtonensis* Lea. Schuylkill [River], Fairmount [Philadelphia, Philadelphia County, Pennsylvania]. Lectotype USNM 86561. Length 97 mm, height 52 mm, width 39 mm (slightly reduced).

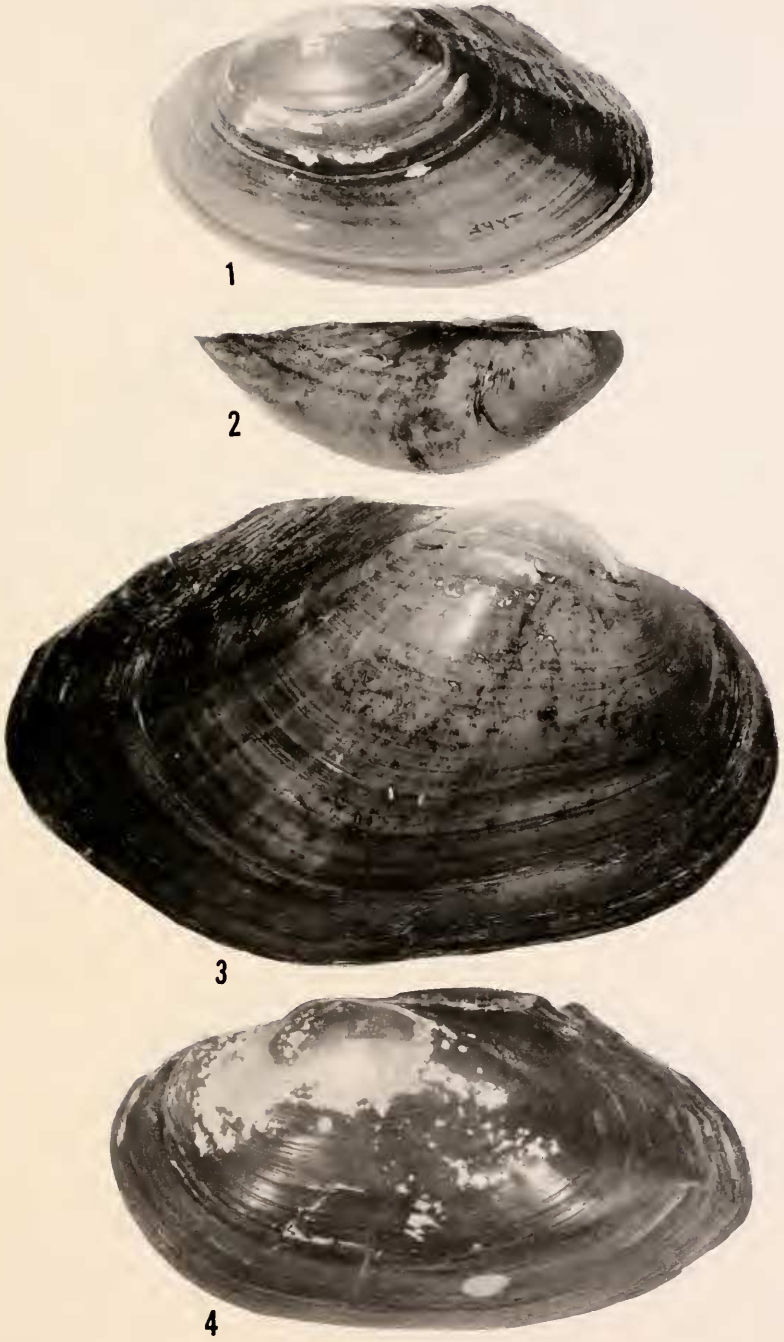
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PLATE 16

Anodonta (Pyganodon) implicata Say

Fig. 1. *Anodonta housatonica* 'Linsley' Gould. Housatonic [River], Corum [= near Huntington, Fairfield County], Connecticut. Holotype USNM 678302. Length 94 mm, height 51 mm, width 34 mm (slightly reduced).

Fig. 2. *Anodonta implicata* Say. Agawam River (outlet of Halfway Pond), Plymouth [Plymouth County], Massachusetts. Neotype MCZ 176769. Length 120 mm, height 60 mm, width 48 mm (somewhat reduced). Interior view, showing the especially distinct pallial line caused by the characteristic anterior-ventral thickening of the shell.

Anodonta (Utterbackia) imbecilis Say

Fig. 3. Magnolia Springs, Perkins, Jenkins County, Georgia. MCZ 234050. Length 90 mm, height 42 mm, width 34 mm (nat. size).

Anodonta (Utterbackia) couperiana Lea

Fig. 4. Pond near Savannah, Chatham County, Georgia. MCZ 119137. Length 87 mm, height 50 mm, width 35 mm (nat. size).


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PLATE 17

Anodonta (Utterbackia) couperiana Lea

Fig. 1. *Anodonta dunlapiana* Lea. [Charleston, Chatham County], South Carolina. Lectotype USNM 86564. Length 83 mm, height 46 mm, width 35 mm (slightly reduced).

Strophitus undulatus (Say)

Fig. 2. Turkey Creek, 8 mi. NW of Edgefield, Edgefield County, South Carolina. MCZ 82807. Length 47 mm, height 29 mm, width 17 mm (nat. size).

Fig. 3. As above. Length 74 mm, height 44 mm, width 27 mm (nat. size).

Carunculina pulla (Conrad)

Fig. 4. *Unio pullus* Conrad. Wateree River, South Carolina. Type lost. (Figures after Conrad). Length 33 mm, height 19 mm, width 13.5 mm (nat. size).

Fig. 5. *Carunculina patrickae* Bates. Savannah River, Johnsons Landing, 10 mi. W of Allendale, Allendale County, South Carolina. Topotype MCZ 255220. Length 32 mm, height 19 mm, width 15.5 mm. Female (1.25 ×). This topotype lacks the sharp posterior ridge of the holotype.

Fig. 6. As above. Length 22 mm, height 13.5 mm, width 10 mm. Male (1.25 ×). This topotype closely resembles Bates' sketch of the allotype.

Fig. 7. University Lake, an impoundment on Morgan Creek, 1 mi. W of Chapel Hill, Orange County, North Carolina. MCZ 261347. Length 25 mm, height 17 mm, width 11 mm. Male (1.25 ×).

Villosa villosa (Wright)

Fig. 8. St. Marys River, Nassau County, Florida. USNM 152066. Length 56 mm, height 29 mm, width 20 mm. Male (slightly reduced).

Fig. 9. *Unio villasus* Wright. Suwannee River [Luraville], Suwannee County, Florida. Lectatype USNM 150503. Length 57 mm, height 28 mm, width 18 mm. Female (slightly reduced).

Villasa vibex (Conrad)

Fig. 10. *Unio vibex* Conrad. Black Warrior River, S of Blount's Spring [Blount County], Alabama. Holotype ANSP 56488a. Length 49 mm, height 28 mm, width 17 mm. Male (approximately nat. size).

Fig. 11. As above. Allotype ANSP 56488. Length 54 mm, height 31 mm, width 19 mm. Female (approximately nat. size).

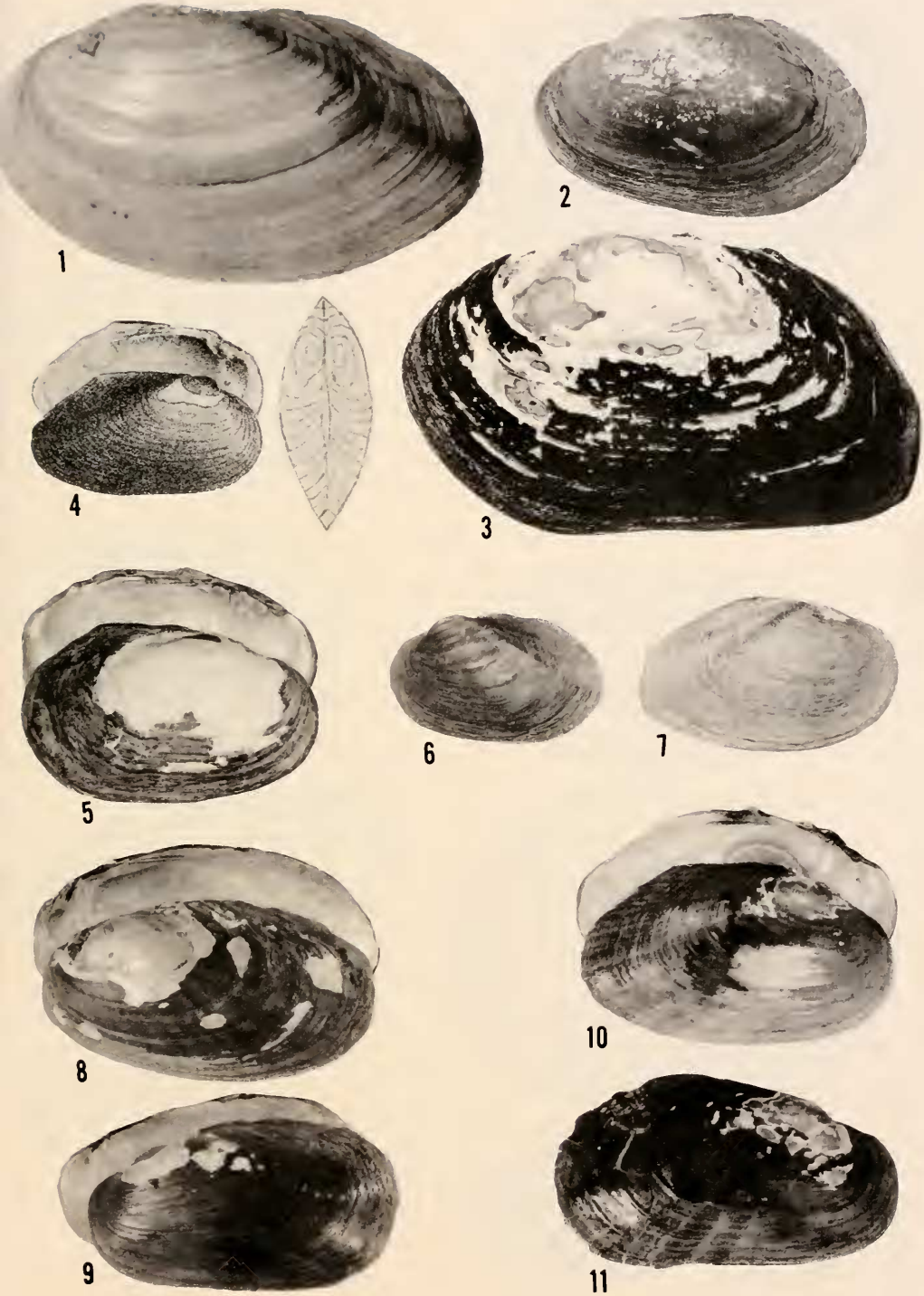
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PLATE 18

Villasa vibex (Conrad)

Fig. 1. *Unio graciliar* Lea. Buckhead Creek [Burke County]; or Tobesaufke [Tobesafkee] Creek, near Macon [Bibb County]; *bath* Georgia. Holotype USNM 85088 [exact locality not indicated]. Length 50 mm, height 28 mm, width 18 mm. Male (slightly reduced).

Fig. 2. *Unio modialiformis* Lea. Santee Canal, South Carolina. Probable holotype USNM 85029. Length 68 mm, height 40 mm, width 25 mm. Female (slightly reduced).

Fig. 3. Mill Race, 2 mi. N of Sardis, Burke County, Georgia. MCZ 234263. Length 48 mm, height 27 mm, width 17 mm. Male (nat. size).

Villasa delumbis (Conrad)

Fig. 4. *Unio concavus* Lea. Abbeville District [Savannah River drainage], South Carolina. Holotype USNM 85154. Length 55 mm, height 32 mm, width 21 mm. Male (slightly reduced).

Fig. 5. *Unio genuinus* Lea. Bissels Pond, Charlatte [Mecklenburg County], North Carolina. Holotype USNM 85123. Length 52 mm, height 30 mm, width 20 mm. Male (slightly reduced).

Fig. 6. Mill Race, 2 mi. N of Sardis, Burke County, Georgia. MCZ 234340. Length 53 mm, height 30 mm, width 19 mm. Male (nat. size).

Fig. 7. As above. Length 57 mm, height 36 mm, width 19 mm. Female (nat. size).

Fig. 8. *Unio ageecheensis* Conrad. Ogeechee River, Georgia. Lectotype MCZ 146971. Length 64 mm, height 39 mm, width 30 mm. Female (approximately nat. size).

Villasa constricta (Conrad)

Fig. 9. *Unio lienosus constrictus* Conrad. North [= Maury] River, Rockbridge County, Virginia. Lectotype ANSP 56465a. Length 41.4 mm, height 27 mm, width 16 mm. Female (approximately nat. size).

Fig. 10. *Unio genthii* Lea. [Probably from] Deep River, Gulf [Chatham County], North Carolina. Holotype USNM 84834. Length 39 mm, height 27 mm, width 18 mm. Male (nat. size).

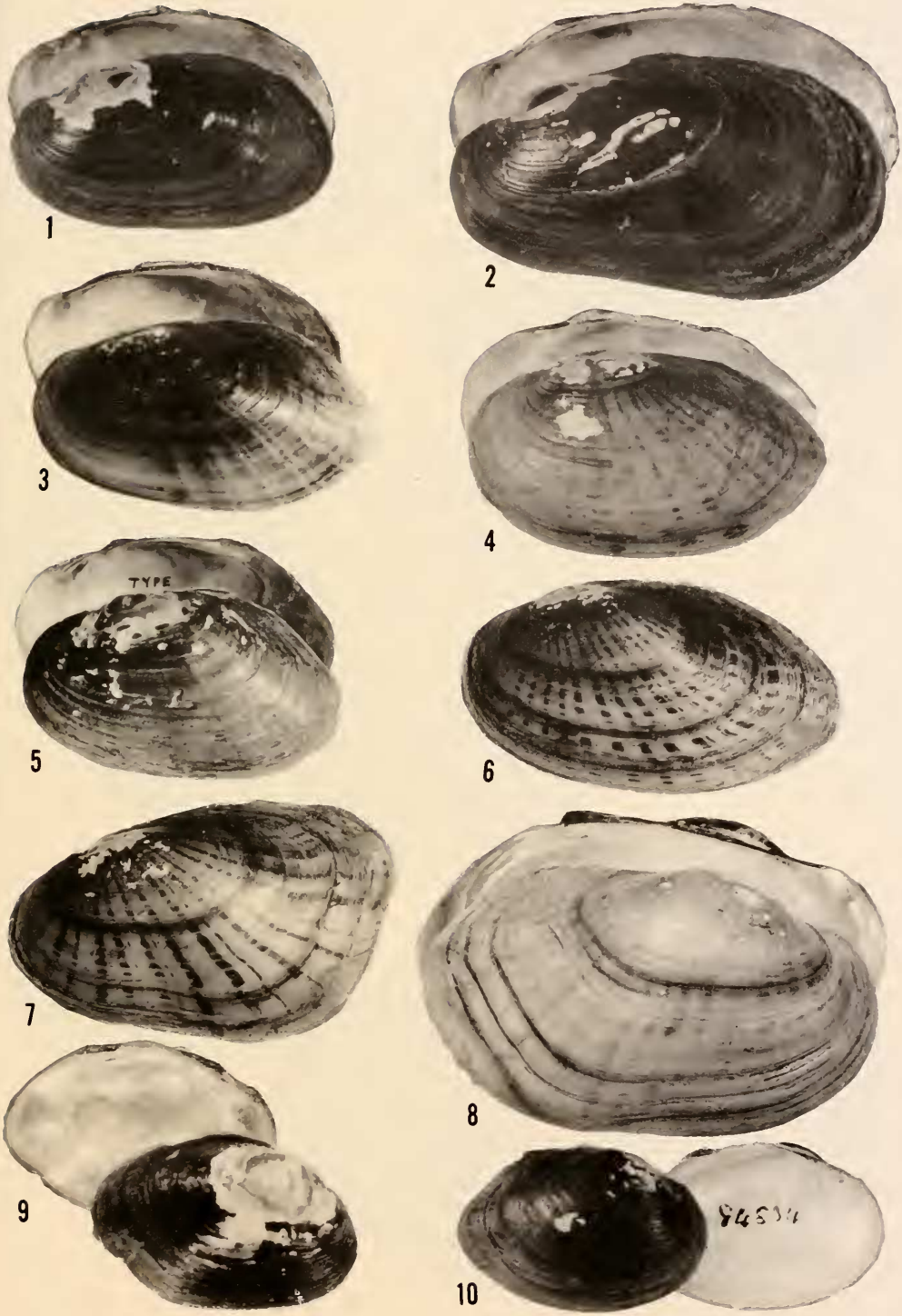
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PLATE 19

Ligumia nasuta (Say)

Fig. 1. Potomac River, Washington, D.C. MCZ 119087. Length 62 mm, height 25 mm, width 12 mm. Male.

Fig. 2. As above. MCZ 5653. Length 66 mm, height 29 mm, width 14 mm. Female.

Lampsilis (*Lampsilis*) *cariosa* (Say)

Fig. 3. Savannah River, 7 mi. NE of Newington, Screven County, Geargia. MCZ 234241. Length 98 mm, height 62 mm, width 42 mm. Male (slightly reduced).

Fig. 4. As above. Length 98 mm, height 69 mm, width 45 mm. Female (slightly reduced).

Fig. 5. *Unio cracatus* Lea. Savannah River, Geargia. Halotype USNM 84908. Length 42 mm, height 27 mm, width 19 mm. Male (slightly reduced).


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PLATE 20

Lampsilis (*Lampsilis*) *dolabraeformis* (Lea)

Fig. 1. Altamaha River, 11 mi. N of Odum, Wayne County, Georgia. MCZ 234197. Length 16 mm, height 12 mm, width 7.5 mm. Male (4×).

Fig. 2. Altamaha River, 10 mi. N of Baxley, Appling County, Georgia. MCZ 234010. Length 91 mm, height 69 mm, width 49 mm. Female (slightly reduced).

Fig. 3. As above. Length 79 mm, height 63 mm, width 50 mm. Male (slightly reduced).

Fig. 4. *Unia dolabraeformis* Lea. Altamaha River, Liberty [now Long] County, Georgia. Holotype USNM 84888. Length 116 mm, height 79 mm, width 51 mm. Male (reduced).

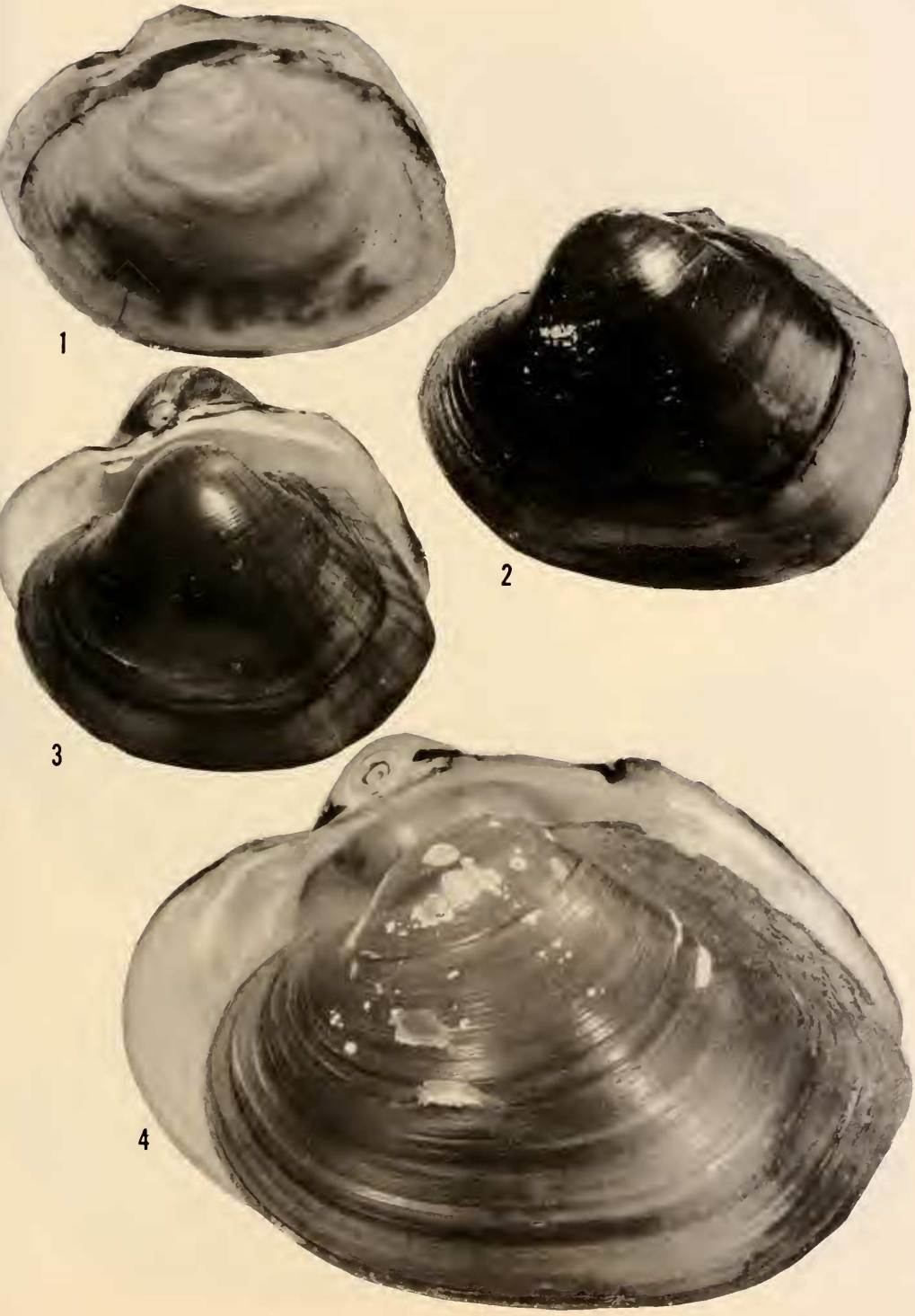
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PLATE 21

Lampsilis (*Lampsilis*) *ovata* (Say)

Fig. 1. *Lampsilis ventricasa cohongaronta* Ortmann. Potomac River, Hancock, Washington County, Maryland. Lectotype Carnegie Museum 61.3999. Length 95 mm, height 60 mm, width 41 mm. Male.

Fig. 2. As above. Allotype Carnegie Museum 61.4000. Length 87 mm, height 62 mm, width 42 mm. Female.

Lampsilis (*Lampsilis*) *achracea* (Say)

Fig. 3. *Unio rosaceus* Conrad. Savannah River, Georgia. Holotype MCZ 178779. Length 73 mm, height 44 mm, width 27 mm. Male (approximately nat. size).

Fig. 4. Lake Waccamaw, [town of] Lake Waccamaw, Columbus County, North Carolina. MCZ 234327. Length 40 mm, height 30 mm, width 17 mm. Female (approximately nat. size).

Fig. 5. As above. Length 50 mm, height 35 mm, width 21 mm. Male (approximately nat. size).

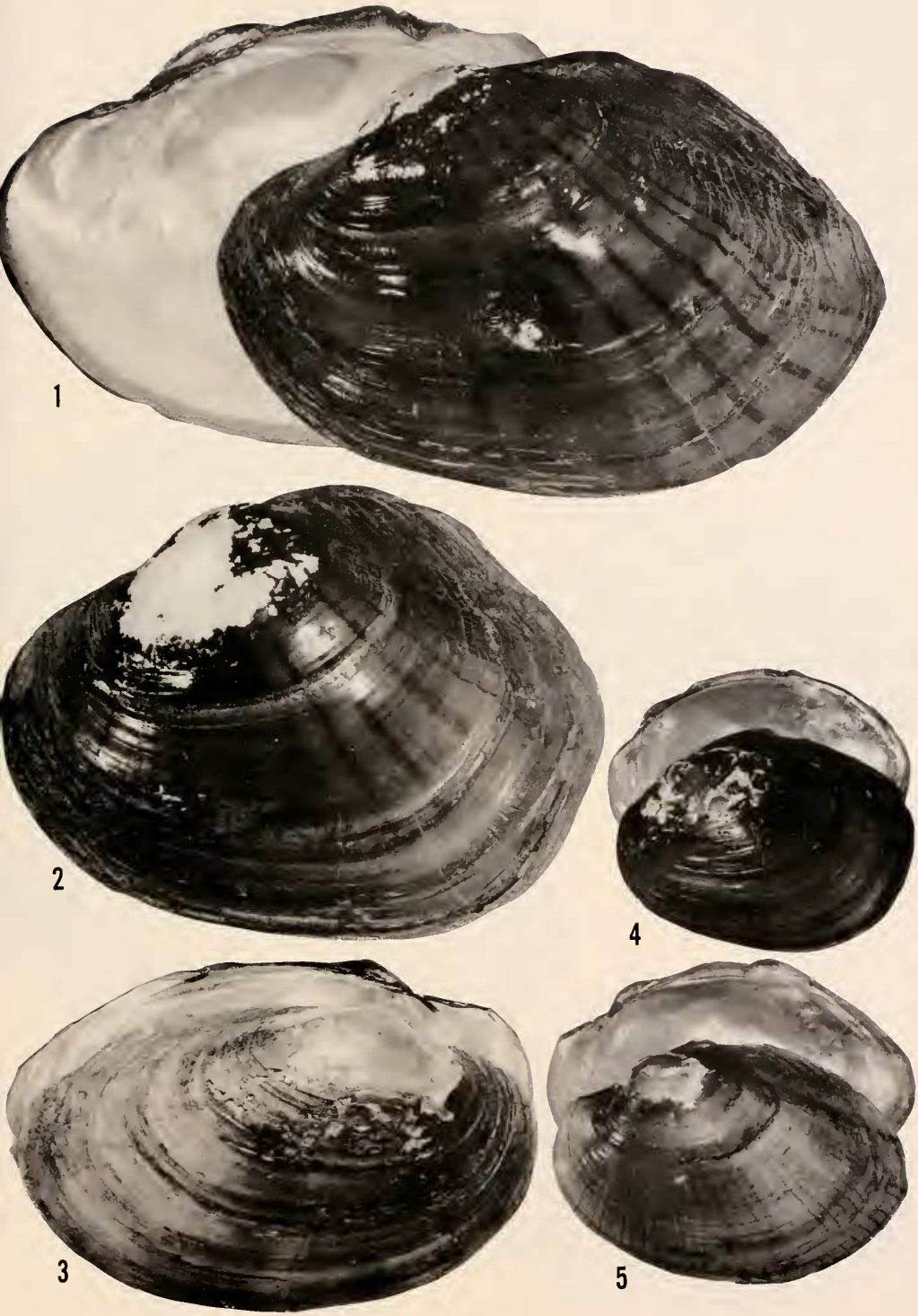
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PLATE 22

Lampsilis (Lampsilis) radiata radiata (Gmelin)

Fig. 1. *Unio conspicuus* Lea. Yadkin River, Salisbury [Rowan County], North Carolina. Holotype USNM 85056. Length 112 mm, height 64 mm, width 39 mm. Male (slightly reduced).

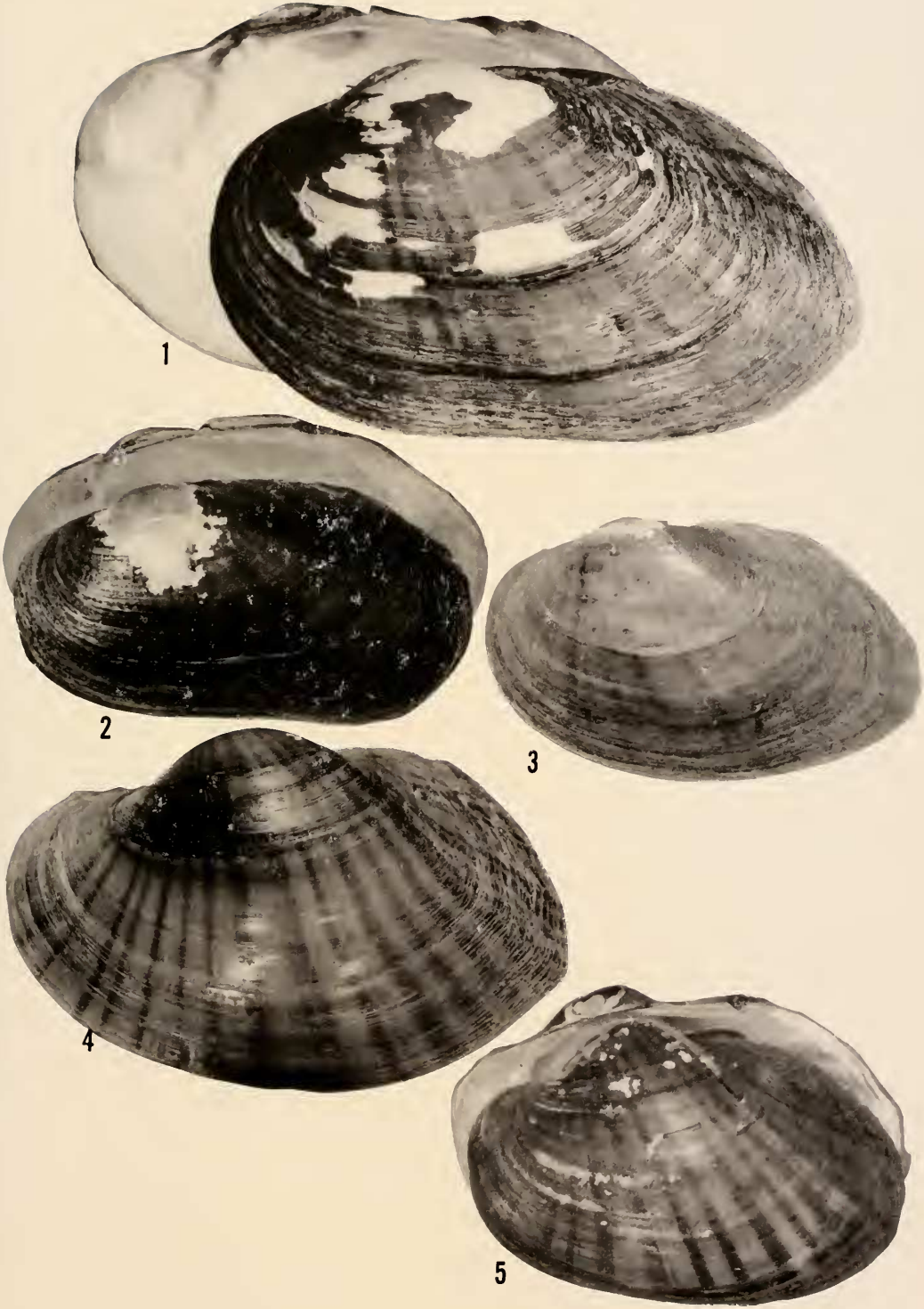
Fig. 2. Greenfield Pond, Wilmington [New Hanover County], North Carolina. USNM 523976. Length 70 mm, height 43 mm, width 28 mm. Male (slightly reduced).

Fig. 3. As above. USNM 452041. Length 76 mm, height 40 mm, width 28 mm. Female (slightly reduced).

Lampsilis (Lampsilis) splendida (Lea)

Fig. 4. Ocmulgee River, 1 mi. S of Lumber City, Telfair County, Georgia. MCZ 234019. Length 71 mm, height 47 mm, width 35 mm. Female (approximately 1.2 ×).

Fig. 5. *Unio splendidus* Lea. Altamaha River [McIntosh or Long County], Georgia. Holotype USNM 84893. Length 70 mm, height 43 mm, width 36 mm. Male (slightly reduced).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